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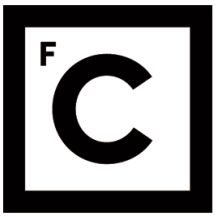

Ciências
ULisboa

Tropical forest fragmentation: effects on the spatio-temporal dynamics of its bat communities

Doutoramento em Biologia
Especialidade de Biologia da Conservação

José Ricardo Teixeira Rocha

Tese orientada por:
Doutor Christoph Friedrich Johannes Meyer
Professor Doutor Jorge Manuel Mestre Marques Palmeirim
Professora Doutora Maria del Mar Cabeza Jaimejuan

Documento especialmente elaborado para a obtenção do grau de doutor

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Fundação para a Ciência e a Tecnologia

2017

This study was funded by Fundação para a Ciência e a Tecnologia, through a PhD scholarship SFRH/BD/80488/2011 and the research project grant project grant PTDC/BIA-BIC/111184/2009. Additional funding was provided by Bat Conservation International through a Student Research Scholarship.

Notas prévia

A presente tese apresenta artigos científicos já publicados ou submetidos para publicação (capítulos 2 a 5), de acordo com o previsto no nº 2 do artigo 25º do Regulamento de Estudos de Pós-Graduação da Universidade de Lisboa, publicado no Diário da República, 2.ª série — N.º 57 — 23 de Março de 2015. Uma vez que estes trabalhos foram realizados em colaboração o candidato esclarece que participou integralmente na conceção dos trabalhos, obtenção dos dados, análise e discussão dos resultados, bem como na redação dos manuscritos.

Lisboa, Dezembro de 2016

José Ricardo Teixeira Rocha

"Reserve 1202 is part of a whole archipelago of Amazonian islands, all with equally clinical-sounding names: Reserve 1112, Reserve 1301, Reserve 2107. Some of the reserves are even smaller than twenty-five acres; a few are quite a bit bigger. Collectively, they represent one of the world's largest and longest-running experiments, the Biological Dynamics of Forest Fragments Project or, for short, the BDFFP. Pretty much every square foot of the BDFFP has been studied by someone: a botanist tagging trees, an ornithologist banding birds, an entomologist counting fruit flies. When I visited Reserve 1202, I ran into a graduate student from Portugal who was surveying bats. At noon he had just recently woken up and was eating pasta in a shed that served as a research station-cum-kitchen. While we were talking, a very skinny cowboy rode up on an only slightly less skinny horse. He had a rifle slung over one shoulder. I wasn't sure whether he'd come because he'd heard the truck I'd arrived on and wanted to protect the student from possible intruders, or because he sensed that there was pasta."

Elizabeth Kolbert
The Sixth Extinction: An Unnatural History

Acknowledgments

Someone once said that "*a journey is best measured in friends, rather than miles*". Well, I somehow feel that something similar can be said about PhDs. I have been lucky enough to have a PhD that has been a journey both in the figurative and literal sense. This marvelous journey has been shared with many friends that have greatly contributed for it to be much more enjoyable that it would otherwise have been. Words fall short to express my gratitude but in the following lines I'll do my best to express how thankful I am to all those colleagues, institutions and friends that have been part of making this dream come true.

First and foremost, I want to thank my outstanding team of supervisors: **Christoph Meyer, Jorge Palmeirim** and **Mar Cabeza.** Each one of you has been important on its own way and I would not have been able to navigate through the waters of this PhD without your vision, guidance, inspiration, support and friendship.

Of my three supervisors the first I have met was **Palmeirim**, during a fieldtrip to Doñana National Park back in 2005. He sat on the back of the bus and during a fair share of the way he shared stories of his adventures in Africa, the Amazon and a few other exotic places. What an impression that made on me. I already knew I wanted to visit some of those places but hearing his stories made me realize I could raise the bar. Why not aim to work in such places as well? Palmeirim, your inspiration has been key for my decision to dive into tropical ecology and throughout these years your enthusiasm for debating anything related to ecology and your love for conservation issues has been truly contagious. It was an enormous pleasure to do fieldwork with you and I am very grateful for all your suggestions regarding the analyses and feedback on the writing.

Mar I met during my MSc. We came across each other at the Cambridge Students Conference in Conservation Science back in 2008. At the time I mentioned that I would love to apply for a scholarship to spend some time in Finland and asked if she would be keen to act as my supervisor. Well… 8 years have passed and in the meantime a project looking into protected area effectiveness in Madagascar developed into several collaborations spanning from the Amazon, to Madagascar and, more recently, Kenya. Mar, I admire so much your energy, commitment and research ethics. Ever since my

internship in Finland you have been pivotal to my career path, always ready to provide thoughtful advice, always keen to build bridges not only between researchers but also between research fields. Somehow you have this amazing capacity of translating what sometimes feels like disconnected thoughts into something that actually makes sense but, of all your qualities, the one that strikes me the most is your humane side. The way you're always ready to help others, me included. Unfortunately, you're yet to discover the amazing diversity of Amazonian bats but it has been trilling to see your enthusiasm for their African counterparts. I had tremendous fun working with you and you helped me like no other to grow as a scientist and as an individual. Thank you for that.

Last but not least, **Christoph**. I am so grateful you managed to find your way to Portugal! This thesis would have never happened without your vision, teaching and much appreciated support. I am utterly thankful for the trust you have put on me since the beginning of the project. Looking now back I can see how green and inexperience I was when we first jumped into the plane heading to the Amazon. Even so, from the beginning you made me feel more like a colleague than an apprentice. I have been struck by your humbleness, acute thinking and scientific curiosity and I am extremely thankful for your friendship! I am proud to have been your first PhD student and I want you to know that you're the kind of supervisor most students would like to have! It has been a fun ride and I truly hope we'll continue to collaborate in the years to come.

Needless to say I am extremely grateful for to the collaborators that contributed to make different sections of this thesis much more significant than would have been otherwise. Much of the work presented here was only possible due to the datasets provided by **Erica Sampaio** and **Paulo Bobrowiec** and to vegetation layers provided by **João Carreiras**. A special thanks is due to **Otso Ovaskainen** for leading the work regarding the application of the hierarchical join species models used in chapter 4 and 5.

The nearly two and a half years of fieldwork that led to this thesis have been shared with a rather large amount of colleagues and friends that have played a pivotal role in the acquisition of the data here presented. Some, like **Inês Silva, Milou Groenenberg, Fábio Farneda** and **Diogo Ferreira** were doing their MSc thesis, whereas others, like **Julia Treitler, Gilberto Fernandez, Madalena Boto, Oriol Massana Valeriano, Iolanda Guerra** and **Marta Acácio** joined as volunteers. All have exceeded themselves during the time in the Amazon and regardless of the extremely demanding field conditions were

always keen to add a couple of hours to the day and take the work a step further. Many of the moments we shared will forever be carved in my memory and in my hearth. I thank you for all for contributing for my time in Brazil to have been so enjoyable! Here, a special thanks is due to **Madalena** and **Oriol** for allowing me use the gorgeous photos they took during their time in the field – some of which can be seen in this thesis and another to **Diogo**, for giving me the opportunity to co-supervise his MSc thesis, it was a tremendous pleasure and a great learning experience.

I am extremely thankful for the support given by the ***Instituto Nacional de Pesquisas da Amazônia (INPA)*** and by the **Biological Dynamics of Forest Fragments Project (BDFFP)**, especially **José Luís Camargo, Ary Ferreira** and **Rosely Hipólito** for all the logistic support given throughout the project. Pivotal for this project was **Paulo Bobrowiec**, whom since the first moment was a key participant in the organization of the field logistics and has provided critical suggestions to the improvement of this thesis. Key for the success of the fieldwork were our amazing field guides **Alaércio Reis, Osmaildo Silva** and **José Tenaçol** and our drivers **Luiz Queiroz** and **Josimar Menezes. Rodrigo Marciente, Kevina Vulinec, Joana Carvalho, Solange Farias, Leonardo Oliveira, Ileana Mayes** and **Ubirajara Capaverde** also joined us multiple times in the field contributing with their time and dedication for the results here presented.

My time in Brazil was also marked by the kindness of **Pedro Santos**, that hosted me (free of charge!) during my first two months of fieldwork and helped me expanding my appreciation for the music of *Chico Burque* and other classic Brazilian beats, by **Douglas Pinheiro**, an outstanding housemate and cherished friend, by **Filipa Palmeirim**, that allowed me to shortly experience the wonderful world of the giant river otters and Amazon river dolphins at the massive Balbina dam, by **Sofia Ponce de Leão** that provided me with a roof during the last few months of fieldwork and guided me through the cultural life of Manaus, and by the American and Brazilian bird teams working at the BDFFP. Among the American team, special thanks to **Luke Powell** and **Jared Wolf** for some enjoyable moments both in the field and out of it, and amongst the Brazilian team special thanks to **Aída Rodrigue, Gonçalo Ferraz, Ulisses Camargo, Francisco Diniz** and **Gabriel McCrate** – it has been a tremendous pleasure to share this experience with you! **Aída**, please feel free to continue to make fun of my Portuguese accent in the years to come.

From the hot and humid tropics this PhD journey took me back to the **Metapopulation Research Center (MRC)** and to Finland. What an amazing place this is. Ilkka Hanski has made an outstanding work by creating such a stimulating environment. Needless to say I love the country and I deeply cherished being back. Many of my memorable moments in the country are due to **Mar's Global Change and Conservation Group (GCCG)** members, namely: **Johanna, Henna, Erin, Marisa, Aili, Álvaro, Sara, Antti, Attila, Annika, Piia, Johannes, Jani, Katarina, Heini, Cristina, Juan, Silvija** and **Maria** and to the extra GCCG pulla (Finnish buns) journal club members such as **Dani, Enrico, Joona, Andrea, Victoria, Peter, Aija, Tiina** and **Ninni**. Thanks for your friendly similes, insightful discussions and fun moments! I learned a lot by debating conservation with many of you! Special thanks to **Dani, Juan, Sara** and **Álvaro** for inviting me to see brown bears and **Sana** for taking me to see flying squirrels! Special thanks also for **Erin, Juan** and **Cristina** for an extremely fun earthworm expedition across the Arctic Circle when I desperately needed a break from data analysis. Lastly, thanks to **Aki Antila**, for introducing me to the birds of Finland, to the Finnish culture and, most importantly, for his warm friendship!

The final stage of this PhD was divided between Lisbon, Manchester and more recently Madeira. Of the time spent in Lisbon am grateful to my office and team colleagues, namely **Ana Leal, Ricardo Martins, Bruno Carreira, Ana Rainho, Ricardo Lima, Tiago Marques, William Douglas, Nuno Pedroso, Miguel Rosalino** and **Inês Rosário**. Thanks for creating a good work environment, for all the help with bureaucracy and other PhD and non-PhD related matters. The time spent in FCUL was deeply enriched by the interaction with many other PhD students and researchers. Lunch time conversations were especially enjoyable and for that I thank **Inês Orfão, Silvia Ceasu, Laetitia Navarro, Joana Carvalho, Susana Varela, Luís Borda-de-Água, Adriana Silva, Manuel Sapage, Jorge Henriques, Sara Silva** and many others. Basketball and ultimate frisbee games were good fun!

This journey would not have been the same without my old FCUL friends. Amongst those, especial thanks to **Andreia Penado, Marta Sampaio, Aurora Santos, Nidia Fernandes, Sasha Vasconcelos, Mariana Campos, Ana Queirós, Gonçalo Rosa** and so many others. It has been a privilege to grown alongside you both as an individual and professionally. Of my non-FCUL friends I am especially thankful to **Filipe Tavares, Patricia Bastos** and **Alexandre Leitão** for being the best flat mates one could ask for and

Dália Bodelgo for being such and inspiration and ray of sunlight. Thanks also to **Joana Ribeiro** that has been such a key person during much of the second half of this PhD. You have all deeply contributed for maintaining my mental health through this process and for me to feel such at home in Lisbon, thanks for that! **Sasha**, thanks once more for the multiple times you commented on my English and for you greatly appreciated friendship.

From my time in Manchester I am thankful for the kindness of **Adrià** and **Eva** for hosting me during the first weeks and showing me around the city. For the first time I managed to work with European bats, and for that I am grateful for the **South Lancashire Bat Group,** especially to **Steve** and **Fiona Parker** and **Baptiste Chadeyron**. It was heartwarming to see your passion for bats! Time spent in Manchester was also marked by the fun moments spent with **James Kemp, Laura Torrent** and **Irene Corenna**.

In last few months in Madeira have been a big learning experience. I am grateful to **Manuela Gouveia** for allowing me the opportunity to lecture at the University of Madeira and **José Jesus** for being such a good colleague and for so many interesting discussions. Thanks also to the **students** from whom I have learned loads.

Thanks for my life-long friends, **Fábio Teixeira, Ana Ornelas, Filipa Alves, André Barbeito, Filipe Pires, Mónica Rodrigues, André Velosa, Carlos Sousa, Rodrigo Dias** and **Catarina Cunha**. Thanks for giving my brain a rest away from biology and for providing me a safety net whenever needed! And **Sana Okayasu**, thanks being such a close friend even if being thousands of km away!

***Mãe**, quem diria que passado tanto tempo ainda andaria a apanhar bichos. As palavras escasseiam para expressar o quão grato estou por todos os teus sacrifícios e pelo teu amor incondicional. O que está nesta tese e aquilo que sou é sem dúvida reflexo disso. Muito, muito obrigado por tudo. **Carlota**, obrigado por me aturares todos estes anos, irás certamente ganhar um lugar no céu. **Dalila**, abençoada hora que decidiste vir morar connosco, tem sido um prazer, sinto que ganhei uma irmã mais velha.*

Catarina… I don't even know how to start. We first met soon after I had started working on this PhD project and as the project matured so did your friendship. You have been a constant over these 5 years and many of my most cherished moments in recent times have been shared with you. I'll forever remember the one week working with Amazonian river turtles and the *Quilombola* communities, what an experience. I am so tremendously

grateful for your friendship, kindness and fun-spirit. Your constant support and positive energy surely contributed for my life as a PhD student to be much more enjoyable. You rock!

Adrià, *então e tu pah? Pensavas que me ia esquecer de ti?* What a ride have the last 5 years been! Close encounters with jaguars in the Amazon, running away from hippos in Kenya, flash-floods in Madagascar… fun fun fun! Meeting you has been one of the best things it has ever happened to me! It is so rare to meet someone with whom one so easily connects and with whom work flows so smoothly. Your list of collaborations continues to expand and the more we work together the more amazed I am about your work ethics, energy, willingness to help and your passion for bats (and almost anything nature-related). I am so grateful for everything you have taught me and I am sure that without your constant support and friendship this PhD would have been a much more difficult and surely less fun endeavor. Thank you also for introducing me to **Eva**, what a lovely couple you two make! Hopefully we will continue to work together for many years to come my dear friend.

Lastly, thanks to the **natural world** itself. In the words of Sir David Attenborough "*it seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living*". Oh, and thanks to **Sir David**… what a source of inspiration you have been!

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Abstract

Tropical forest ecosystems harbour more than half of the planet's terrestrial species and are of paramount importance for human well-being. Yet, the persistence of tropical forests and their faunal communities is jeopardised by growing rates of habitat loss, fragmentation and degradation. Bats provide critical ecosystem services to tropical forest and are thus crucial for the maintenance of healthy forest habitats. However, as with many other taxa, they are increasingly threatened by anthropogenic forest modification.

The main aim of this thesis was to investigate the spatio-temporal effects of forest fragmentation on tropical forest bats. The study was based at the Biological Dynamics of Forest Fragment Project (BDFFP), a whole-ecosystem experiment implemented in the Central Brazilian Amazon. The BDFFP bat fauna was initially studied in 1996-2002, allowing for a comparative follow-up study capable of unveiling the combined effects of spatial and temporal heterogeneity on tropical bat assemblages in fragmented forest landscapes. The controlled experimental setting provided by the BDFFP was further used to investigate the relative roles of vegetation structure and landscape composition and configuration on bat communities, and the depth of this analysis was extended by the examination of sex-specific responses to both local- and landscape-level attributes. Additionally, the re-isolation of forest fragments in late-2013 enabled a before and after re-isolation comparison, allowing valuable insights into short-term responses to abrupt changes in matrix structure.

The regeneration of the secondary forest surrounding the BDFFP fragments buffered some of the pervasive consequences of forest fragmentation, however, more than 30 years after initial deforestation bat communities still exhibited scale-sensitive and sex-specific responses to fragmentation. While results highlight the importance of larger (> 10 ha)

forest patches and mature secondary forest (> 20 years) for the conservation of tropical bats, they emphasize the irreplaceable value of vast tracts of primary habitat for the long-term conservation of tropical biodiversity.

Key-words: Amazon, Bats, Edge effects, Fragmentation, Landscape ecology, Rainforest, Secondary forests.

Resumo

Nas últimas décadas temos assistido a significativos avanços na compreensão da resposta de diversos grupos faunísticos à modificação florestal. No entanto, a nossa perceção de como a qualidade do habitat interage com o contexto de paisagem, e como estas afetam de forma conjunta as espécies que habitam regiões tropicais alteradas pela ação humana ainda é limitada e um aumento deste conhecimento é urgente para uma melhor gestão e conservação destas mesmas paisagens.

Os morcegos são a segunda ordem de mamíferos mais diversa e atingem o auge da sua diversidade taxonómica e ecológica nos Neotrópicos, onde desempenham importantes funções ecológicas. Devido à sua elevada abundância, diversidade funcional e "fácil" amostragem, são um bom modelo biológico para a investigação do efeito da alteração de habitat em florestas tropicais.

Esta tese teve como objetivo principal contribuir para o conhecimento de como comunidades faunísticas tropicais respondem à fragmentação florestal ao longo dos eixos espaciais e temporais. Para tal foram usados morcegos como modelo biológico e os efeitos da fragmentação florestal na sua diversidade, abundância e composição foram estudados na paisagem experimental do Projeto de Dinâmica Biológica de Fragmentos Florestais (PDBFF), na Amazónia Brasileira.

Capítulo 2. Consequências de uma experiência de fragmentação de grande escala para morcegos neotropicais: avaliação da importância relativa da influência das variáveis locais e ao nível da paisagem

Os primeiros estudos relativos ao impacto da fragmentação tiveram as suas raízes na teoria de biogeografia de ilhas e centravam-se essencialmente no estudo da influência do tamanho dos fragmentos e da distância dos mesmos entre si e destes a zonas de habitat não fragmentado. Com o progredir dos anos, avanços teóricos no domínio da ecologia de paisagem levaram a uma maior consideração do arranjo espacial dos fragmentos e da composição da matriz. No entanto, apesar de uma vasta literatura sobre o tema, a maioria dos estudos limita-se a comparar locais no interior de fragmentos com habitats no interior de floresta contínua, fazendo com que estudos que analisem todo o gradiente de perturbação de paisagens fragmentadas (interiores de floresta contínua e fragmentos, bordas florestais e matriz) sejam escassos. Adicionalmente, o real efeito da fragmentação nas comunidades florestais é condicionado pela escassez de estudos que incluam métricas referentes à estrutura da vegetação, variável que se encontra fortemente associada ao grau de degradação do habitat.

Neste capítulo, pretendeu-se investigar como comunidades de morcegos neotropicais respondem à ação conjunta da estrutura da vegetação e da composição e configuração da paisagem em gradientes de perturbação do qual fazem parte o interior de florestas contínuas e fragmentos, bordas florestais e matriz. Assim, com base em mais de 4 000 capturas de 50 espécies, analisou-se a várias escalas, a forma como diferentes métricas de biodiversidade (riqueza específica, dominância e abundância) são afetadas pela estrutura da vegetação e pela quantidade e configuração da floresta primária.

Apesar da matriz relativamente permeável em que os fragmentos do PDBFF são incorporados (composta por vegetação secundária com idade ≥ 16 anos), foi observado que as comunidades de morcegos são afetadas pela área dos fragmentos, e que as respostas a métricas de estrutura da vegetação e de composição e configuração da paisagem variam consoante o grupo funcional e a escala espacial considerada. Os resultados indicam que mesmo em paisagens com uma matriz bastante permeável, os efeitos da fragmentação ainda se fazem sentir e sublinham que a consideração de métricas de paisagem a várias escalas permite uma compreensão mais abrangente dos efeitos da fragmentação em comunidades de vertebrados tropicais.

Capítulo 3. Será que o sexo importa em paisagens fragmentadas? Efeitos deferenciais da fragmentação em machos e fêmeas de morcegos tropicais.

A gestão de paisagens fragmentadas com vista à persistência, de longo prazo, de espécies nativas dos habitats originais é um dos maiores desafios da comunidade conservacionista. No entanto, apesar de machos e fêmeas de várias espécies animais apresentarem diferenças no uso do habitat, as respostas específicas dos diferentes sexos à fragmentação florestal têm sido pouco estudadas.

Neste capítulo, foram estudas as respostas de macho e fêmeas de 8 espécies de morcegos a um gradiente de perturbação florestal incluindo o interior de florestas contínuas e fragmentos, bordas e matriz. Antevendo potenciais efeitos de sazonalidade na resposta de ambos os sexos, analisaram-se de forma independente dados das estações seca e chuvosa e para as duas espécies com maior número de capturas (*Carollia perspicillata* e *Rhinophylla pumilio*), investigou-se ainda, a várias escalas focais, o efeito conjunto da estrutura da vegetação e da composição e configuração da paisagem na abundância.

Os nossos resultados revelam que apesar de ambos os sexos reagirem de forma semelhante ao gradiente de perturbação analisado, para três espécies, machos e fêmeas apresentam respostas diferenciadas em pelo menos uma das estações consideradas. Observou-se ainda que, apesar das proporções entre machos e fêmeas serem equilibradas no interior de floresta contínua e fragmentos, para a maioria das espécies as fêmeas superam os machos na borda e na matriz. Ademais, a resposta da abundância à estrutura da vegetação e composição e configuração da paisagem diferiram entre machos e fêmeas e as diferenças observadas foram consistentemente mais pronunciadas na estação seca. Os resultados deste estudo revelam diferenças consideráveis na resposta de machos e fêmeas à fragmentação e degradação florestal, complementando desta forma o atual conhecimento relativo ao impacto da fragmentação sobre comunidades de vertebrados tropicais.

Capítulo 4. Avaliação do impacto de pequenas clareiras florestais provocadas pela ação humana em morcegos de uma paisagem fragmentada

Nas regiões tropicais a ação humana tem vindo a moldar paisagens nas quais pequenas clareiras de origem antropogénica são características conspícuas. No entanto, várias espécies florestais evitam áreas desflorestadas, mesmo que estas sejam de dimensões modestas (< 30 m de largura). Como tal, a análise do impacto destas perturbações de pequena escala em espécies com hábitos florestais é fundamental para a elaboração de estratégias de conservação eficazes.

Cada 10 anos a equipa de gestão do PDBFF procede ao re-isolamento dos fragmentos florestais através do corte de uma faixa de 100 m de floresta secundária em torno dos mesmos. Neste capítulo, realizou-se uma comparação pré- e pós-reisolamento das

comunidades dos morcegos no interior, borda e matriz de oito fragmentos florestais, bem como em áreas de floresta contínua, que serviram de controlo experimental. Desta forma estudou-se a resposta a curto-prazo dos morcegos, a uma alteração abrupta no contraste entre fragmentos e a matriz. As oito visitas pré- e as quatro visitas pós-reisolamento traduziram-se em mais de 6 000 capturas e a análise de dados, com base em modelos de distribuição conjunta de espécies, permitiu desvendar que o reisolamento teve pouco efeito na riqueza específica, mas, no entanto, teve um efeito considerável na semelhança da composição de espécies entre floresta contínua e habitats modificados (interior, borda e matrix dos fragmentos florestais). A amostragem de áreas de floresta contínua pré- e pós-reisolamento dos fragmentos florestais permitiu desvendar que grande parte da variação na ocupação de espécies entre os dois períodos de mostragem não se deverá dever ao efeito do reisolamento dos fragmentos, mas sim ser um reflexo da variabilidade espacial e temporal natural das comunidades de morcegos tropicais.

Capítulo 5. Efeito da regeneração da floresta secundária em morcegos de uma paisagem fragmentada

As florestas secundárias são atualmente o tipo de coberto florestal mais comum nos trópicos e embora o potencial destas para a conservação da biodiversidade continue a ser debatido, um crescente número de estudos sugere que a regeneração da floresta secundária pode diminuir os impactos de fragmentação em paisagens modificadas.

Neste capítulo, foi estudada a forma como os morcegos do PDBFF foram influenciados pela regeneração da floresta secundária entre ~15 e ~30 anos após o isolamento experimental dos fragmentos.

As comunidades de morcegos do PDBFF foram amostradas pela primeira vez em entre 1996 e 2002 em áreas de floresta contínua, fragmentos florestais e áreas de floresta secundária. De forma a avaliar o efeito da regeneração da floresta secundária na ocupação e abundância de morcegos generalistas e especialistas, estes mesmos locais foram novamente amostrados entre 2011 e 2013. No combinar de ambos os períodos foram capturados mais de 6 000 morcegos de 50 espécies que foram classificadas, de acordo com a sua afinidade para floresta primária, em especialistas e generalistas. A análise de dados, através de modelos de distribuição conjunta de espécies, revelou que enquanto a maturação da floresta secundária teve efeitos positivos nas espécies especialistas, teve por sua vez efeitos insignificantes (nos fragmentos) e negativos (na floresta secundária) sobre as espécies generalistas.

Assim, os nossos resultados enfatizam que o potencial das florestas secundárias para reverter o declínio faunístico em paisagens tropicais fragmentadas aumenta com o aumento da idade dessas mesmas florestas secundárias e que as espécies especialistas, que geralmente são alvo de maior preocupação do ponto de vista da sua conservação, são as maiores beneficiárias da maturação da floresta secundária. Assim sendo, apesar da conservação da floresta primária dever sempre ser priorizada, os resultados deste estudo sugerem que a proteção de florestas secundárias em avançado estado de regeneração (> 20 anos) deve ser incentivada.

Palavras-chave: Amazónia; Conservação; Ecologia de paisagem; Florestas secundárias; Fragmentação; Morcegos.

CHAPTER 1

General introduction

CHAPTER 1

General introduction

If (anthropogenic) "forest fragmentation" brings fear to a conservationist's heart, "tropical forest fragmentation" is nightmare material.

Tropical forest fragmentation

Fragmentation, the process by which previously continuous habitat is broken into smaller habitat patches discordant from the adjacent matrix, is not a new phenomenon nor is it solely an anthropogenic process. In fact, fragmented habitats are commonly occurring features at a range of scales in natural landscapes and examples are as varied as rocky outcrops in grassland environments, water ponds in savannah ecosystems and islands in an oceanic setting. Yet, although habitat fragmentation is at least as old as life itself and has been a key driver of speciation and biological differentiation (Weir and Schluter 2004), fragmentation as a by-product of anthropogenic habitat modification is currently considered as one of the greatest threats to biodiversity worldwide (Ewers and Didham 2006).

The human population is projected to approach 11 billion within our century (United Nations 2016). As human numbers soar, so does our global footprint and much of the projected threats to biodiversity arising from human growth and increasing per-capita consumption are expected to be especially severe for tropical ecosystems, which are already massively disrupted by habitat loss and myriad environmental alterations such as overhunting and climate change (Bradshaw et al. 2008; Wright 2010; Laurance et al.

2014; Malhi et al. 2014). A prime consequence of large-scale land-use transformation associated with human expansion is the division of continuous forest habitats into smaller and more isolated forest patches embedded in a matrix of modified habitat (Haddad et al. 2015). By the synergistic effects of area reduction, increased isolation and greater exposure to habitat deterioration and human activities along its edges, this process of forest subdivision (fragmentation) has pervasive and long-lasting impacts on the function and structure of forest remnants (Ewers and Didham 2006; Fischer and Lindenmayer 2007; Haddad et al. 2015). The contribution of these impacts to the ongoing biodiversity crisis is such that Diamond (1989), in his investigation of the drivers of recent extinctions, included the correlated process of habitat loss and fragmentation in the "evil quartet" (alongside overexploitation, invasive species and chains of extinctions) and the theme is now cornerstone in conservation biology (Ewers and Didham 2006).

Humans have been clearing and modifying forests for Millennia (Williams 2006; Chazdon 2014). Yet, despite massive deforestation, global forest cover amounts to ~53.06 million km^2 (an area more than 3 times the size of Russia) (Riitters et al. 2016), most of which is located in the tropics (Hansen et al. 2013). However, even though large expanses of continuous forests still persist (e.g. in the Amazon and Congo River Basins) (Hansen et al. 2013), a recent analysis of high-resolution global forest cover maps revealed that more than 50% of remaining forest is within 500 m of the forest's edge (of which 20% is within 100 m from the edge) and most of the remaining forest fragments have less than 10 ha (Haddad et al. 2015). Moreover, between 2000 and 2012 global forest loss (2.3 million km^2) far surpassed forest gain (0.8 million km^2) (Hansen et al. 2013), indicating that deforestation and fragmentation continues to rise with the increasing demand for agricultural lands (Wright 2010; Laurance et al. 2014). Although deforestation and forest fragmentation are global phenomena, forest loss is greater in poorer countries and forest

clearance in the tropics has surpassed the rates of all other regions (Sloan and Sayer 2015). In fact, between 2002 and 2012 tropical deforestation amounted to 32% of global forest loss, half of which is taking place in South America (Hansen et al. 2013).

Fragmentation research

As with many other terms in ecology and conservation, "fragmentation" is a multi-faceted concept that embraces numerous, often interacting patterns and processes (Ewers and Didham 2007). Over the last decades this umbrella concept has galvanized abundant empirical and theoretical research on themes as diverse as habitat area (Nupp and Swihart 1996), effects of patch shape and isolation (Tischendorf et al. 2003), edge effects (Ewers and Didham 2008; Ewers and Banks-Leite 2013), matrix influence on connectivity (Powell et al. 2015) or fragmentation effects on ecosystems services (Ferraz et al. 2014), and on a wide array of taxa and study systems (Ewers and Didham 2006). This rich literature has led to considerable conceptual advances (Didham et al. 2012) and the field, supported by plentiful empirical evidence, has now moved far beyond its early roots in MacArthur and Wilson's (1967) island biogeography theory (IBT) (Laurance 2008).

The IBT states that 1) larger islands (to which forest fragments are terrestrial analogues) hold higher species richness than smaller islands; 2) the distance between islands and mainland is inversely related to the island's species richness; and 3) there's a continuous species turnover over time (MacArthur and Wilson 1967). These premises have formed the bedrock to much of the research on forest fragmentation and, as predicted by the IBT, plentiful field data attest to strong area and isolation effects (e.g. Ferraz et al. 2007; Struebig et al. 2008; Meyer and Kalko 2008; Benchimol and Peres 2015) and that fragment communities undergo a process of biological relaxation in which species

diversity declines with time (e.g. Laurance et al. 2011). However, the elegant simplicity of the IBT has the downside of being unable to predict the response of fragment communities to many important biotic and abiotic processes associated with fragmentation such as habitat degradation due to novel ecological boundaries (Laurance et al. 2007), landscape configuration (Villard and Metzger 2014) and the influence of dynamic "*real world*" landscape matrices (Prevedello and Vieira 2010; Watling et al. 2011).

The degree by which the surrounding matrix influences the communities inhabiting forest remnants in anthropogenic fragmented landscapes has attracted increasing attention in recent years and a growing body of evidence now supports that many responses to fragmentation are strongly mediated by matrix quality and permeability (Gascon et al. 1999; Laurance et al. 2007; Mendenhall et al. 2014; Wolfe et al. 2015). Matrix composition affects connectivity (Watling et al. 2011; Powell et al. 2015), which in turn impacts on the demography (Korfanta et al. 2012), gene flow (Struebig et al. 2011), metapopulation dynamics (Vandermeer and Carvajal 2001) and eventually the long-term persistence of local populations. Moreover, the matrix can provide supplementary resources for some species, benefiting some groups but not others, and consequently can lead to distorted species interaction networks and alter within-patch dynamics (Watling et al. 2011).

One of the most ubiquitous features of fragmented forest landscapes is the deterioration in habitat quality near forest edges (Haddad et al. 2015). Here, abiotic gradients and alternative successional pathways alter vegetation structure (Laurance et al. 2011) leading to frequent large-scale changes in biological communities (e.g. Ewers and Didham 2008). The magnitude of these changes is fundamentally influenced by the matrix surrounding

forest fragments, with high structural contrast between fragment and matrix leading to more pronounced edge effects than low-contrast edges (Ewers and Didham 2006).

Across the tropics, vast areas cleared of old-growth undergo secondary succession (Chazdon 2014). Despite considerable difficulties in using remote sensing data to differentiate secondary regrowth from tree plantations and even (for late stages of regeneration) from old-growth, estimates, using high-resolution satellite imagery indicate that between 2000 and 2012 there has been a global increase of 0.25 million km^2 in secondary forest cover (Hansen et al. 2013). In the Neotropics, up to one third of the areas of primary forest annually deforested were estimated to initiate forest regeneration between 2001 and 2010 (Aide et al. 2013). Secondary forests represent therefore a conspicuous (low-contrast) matrix type in many human-modified tropical landscapes and understanding how this land-use type interacts with and likely mediates fragmentation processes is critical for conservation, management and conservation strategies (Arroyo-Rodríguez et al. 2015).

Numerous recent studies suggest that secondary forests act as important reservoirs of tropical biodiversity and an important source of ecosystem functions and services (e.g. Barlow et al. 2007; Gardner et al. 2007; Parry et al. 2007; Goosem et al. 2016). However, most of these studies base their inference on chronosequences - spatially distinct sites with different vegetation age classes – and, while yielding important insights, often lack rigorous controls, randomization and capacity to isolate confounding variables. Long-term, whole-ecosystem experiments, by manipulating specific components of regeneration and fragmentation while controlling for confounding (sometimes correlated and synergistic) factors such as hunting and habitat amount, offer a unique setting in which to undertake longitudinal studies aimed at investigating the ecological mechanisms

that underpin the interaction between forest remnants and secondary forest matrices (Fayle et al. 2015; Haddad et al. 2015).

Research on the often neglected temporal dimension of fragmentation has revealed that, following fragment isolation, short-term crowding effects eventually fade into long-term extinction debts (Ewers and Didham 2006; Driscoll et al. 2013). The realisation that several aspects of fragmentation require time to appear is indicative that fragmentation cannot be studied as a static phenomenon and emphasises the key importance of long-term fragmentation experiments to evaluate the dynamics of fragmented landscapes over long timescales.

Study area: The Biological Dynamics of Forest Fragments Project

The Biological Dynamics of Forest Fragments Project (BDFFP) is a whole-ecosystem manipulation spanning 800 km^2 and located ~80 km north of Manaus, Brazil (S2º30', W 60º; Fig. 1). The project, originally termed the Minimal Critical Size of Ecosystems project, was initiated in 1979 by Thomas E. Lovejoy with the intention of addressing the SLOSS (Single Large Or Several Small) debate by investigating how much forested area was needed to preserve species composition and species interactions unaffected by forest fragmentation (Bierregaard Jr. and Gascon 2001). The experiment has been running continuously ever since and is now the world's longest-running experimental study of habitat fragmentation, being currently managed by the National Institute of Amazonian Research (INPA) in collaboration with the Smithsonian Tropical Research Institute (Laurance et al. 2016).

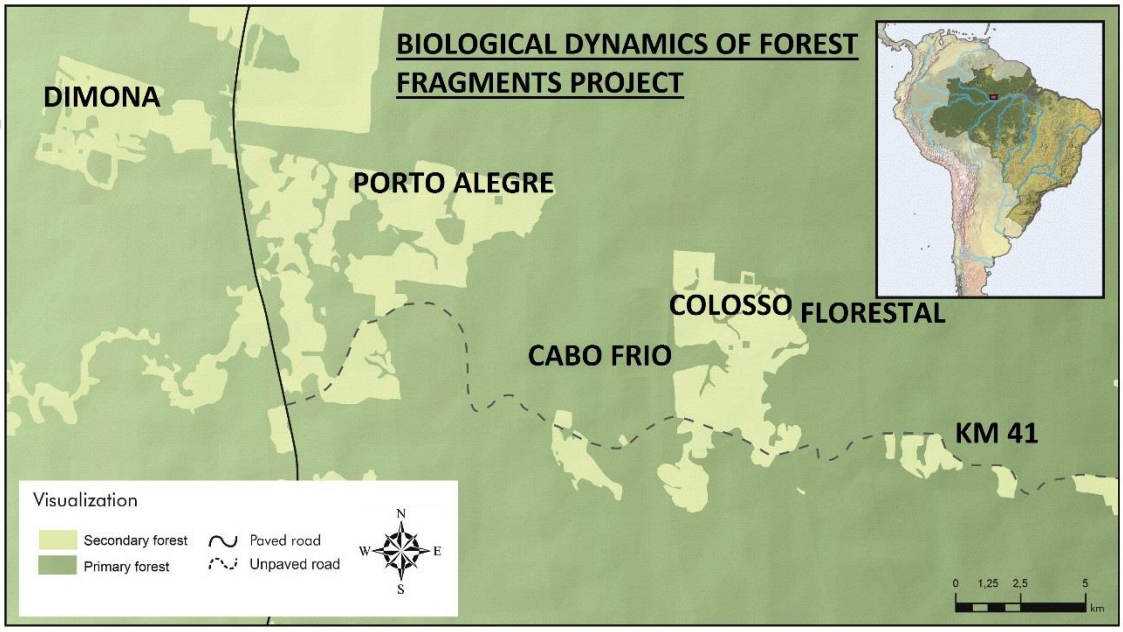

Figure 1 - Map of the Biological Dynamics of Forest Fragments Project (BDFFP) study area in the Central Amazon. Dark green: primary forest fragments and continuous primary forest; light green: secondary forest matrix.

In the late-70s the BDFFP study area was due to be cleared for cattle ranching under subsidies by the Brazilian federal government in order to boost the region's economic development. Legislation at the time determined that an area equivalent to 50% of the primary forest of a given property had to be retained. Aware of this, Thomas E. Lovejoy with the support from the Word Wildlife Fund-US, coordinated efforts with the ranchers to experimentally isolate pockets of old-growth forest as land was cleared by cutting and burning. Logistical and economic drawbacks restrained the project to 11 of the originally intended 24 reserves and eventually dictated the end of cattle ranging activities, allowing the regrowth of much of the area previously cleared. The secondary vegetation around the experimentally isolated forest fragments is currently dominated by *Vismia* spp. (areas that were cleared and burned) and *Cecropia* spp. (areas that were cleared without fire)

(Mesquita et al. 2015). Fragments have been re-isolated on 4 to 5 occasions (one of which during this study) by clearing and sometimes burning (Laurance et al. 2011). The 11 experimental fragments are grouped in three size classes: 1 ha (five fragments), 10 ha (four fragments) and 100 ha (two fragments). Their distance from continuous forest ranges from 70 to 1000 m (Fig. 1).

The BDFFP experimental landscape is classified as unflooded *terra firme* Amazonian forest. It has a mean annual temperature of 26ºC (minimum 19-21ºC and maximum 35-39 ºC) (Oliveira and Mori 1999) and receives 1900-3500 mm of rain annually. There is a rainy season from November to June (when monthly precipitation can exceed 300 mm) and a dry season from July to November (when monthly precipitation drops below 100 mm) (INPA 2014). Flowering and fruiting peaks take place during the dry season and at the beginning of the wet season, respectively (Haugaasen and Peres 2005). The dominant soil type is yellow latosols, which are acidic, well-drained and nutrient-poor (Laurance et al. 2011). The topography is relatively flat (80-160 m elevation) and the primary forest canopy reaches 30-37 m, with emergent trees up to 55 m (Laurance et al. 2011). Tree species richness (diameter at breast high ≥ 10 cm) can exceed 285 species per ha (Oliveira and Mori 1999).

This study included eight forest fragments (three of 1 ha, three of 10 ha, two of 100 ha – distributed in Dimona, Porto Alegre and Colosso camps), nine control sites in three areas of continuous forest (Cabo Frio, Florestal and Km 41 camps) and several sites in the regenerating secondary forest matrix (Fig. 1).

For a more detailed description of the study area, experimental manipulation and research outcomes see Laurance et al. (2011; 2016).

Neotropical bats

At present, more than 1 300 species of bats are known to science (Fenton and Simmons, 2014) and, following a commonly observed biogeographic pattern, bat diversity rises with increasing proximity to the equator and peaks in tropical regions (Altringham 2011). The Neotropics of South and Central America constitute the planet's epicenter of chiropteran diversity with close to 300 species and more than 80 genera (Mickleburgh et al. 2002). Within the region, the Amazon basin is especially rich, harboring more than one in ten of the world's known bat species (Bernard et al. 2011a) (Fig. 2). Indeed, in some Central Amazonian localities more than 100 species can be found living sympatrically (Rex et al. 2008).

Figure 2 - Geographic variation in bat species richness across Latin America. Sources: IUCN and Bat Conservation International.

Bats are divided into 17 families, of which nine (Phyllostomidae, Thyropteridae, Furipteridae, Noctilionidae, Mormoopidae, Emballonuridae, Vespertilionidae, Molossidae, and Natalidae) can be found in the Neotropics (Altringham 2011). Species distribution across Neotropical bat families is rather uneven with the majority of species belonging to the family of New World leaf-nosed bats (Phyllostomidae), the ecologically most diverse family within the order with nearly 200 recognized species across Central and South America (Gardner 2007) (Fig. 3).

Bats are key providers of many ecosystem services such as seed dispersal, pollination and regulation of small vertebrate and invertebrate populations (Kunz et al. 2011). They are key elements of the intricate ecological networks of tropical ecosystems and, in both pristine and human-modified landscapes frugivores, the phyllostomid subfamilies Stenodermatinae and Carolliinae, play pivotal roles as "forest gardeners" by dispersing seeds far and wide and, by doing so aid maintaining plant diversity and promote secondary forest succession (de la Peña-Domene et al. 2014). Some other species (such as Glossophaginae), hover like hummingbirds in front of several plant species and with their long muzzles and tongues probe flowers to extract their nectar, effectively acting as pollinators, and therefore facilitating reproduction and helping to maintain the genetic diversity of flowering plants (Quesada et al. 2004). Most Neotropical bats are either obligate or facultative insect-eaters, gleaning insects and other arthropods directly from the vegetation in the forest understory or capturing prey in open space, above and below the forest canopy. By doing so they greatly reduce arthropod-related herbivory (Maas et al. 2015) and redistribute nutrients through their guano, helping to maintain terrestrial and aquatic ecosystems (Iskali and Zhang 2015). In the Neotropics four species of phyllostomids, namely the greater spear-nosed bat *Phyllostomus hastatus*, the fringe-lipped bat *Trachops cirrhosus*, the big-eared woolly bat *Chrotopterus auritus* and the spectral bat *Vampyrum spectrum*, are confirmed carnivores (e.g. Rocha et al. 2012; Rocha et al. 2016) and the two species of *Noctilio* are fish-eaters. Bats themselves are on the menu of several groups including spiders, giant centipedes, frogs, marsupials, other bats, birds and snakes (e.g. Rocha and López-Baucells 2014).

Figure 3 – Rostrum of several Amazonian phyllostomids. A) *Mimon crenulatum*; B) *Lophostoma brasiliense*; C) *Lonchophylla thomasi*; D) *Desmodus rotundus*; E) *Ametrida centurio*; F) *Tonatia saurophila*; G) *Dermanura gnomus* H) *Chrotopterus auritus;* I) *Artibeus obscurus*; J) *Artibeus litutatus*; K) *Lampronycteris brachyotis*; L) *Mesophylla macconnelli*; M) *Carollia perspicillata*; N) *Micronycteris sanborni*; O) *Lophostoma silvicolum*; P) *Lophostoma carrikeri*; Q) *Trachops cirrhosus*; R) *Chiroderma trinitatum*; S) *Trinycteris nicefori* and T) *Glyphonycteris daviesi*. All photos by Adrià López-Baucells and Oriol Massana.

In recent years several new species have been described and new records have extended the geographic range of some species by hundreds of kilometers (such as the recent records of *Lasiurus egregius* and *Micronycteris sanborni* at the BDFFP (López-Baucells et al. 2013; 2014). However, knowledge on Neotropical bats is still limited and extremely biased to some relatively well-studied localities such as the BDFFP and the Barro Colorado Island in Panama (Bernard et al. 2011b; Kalko et al. 2008).

Neotropical bats and fragmentation

Bats, as many other taxa, are under threat from habitat loss and fragmentation and this is especially true for tropical rainforest communities, which are particularly species rich (Mickleburgh et al. 2002). As stated above, bats occupy a wide range of trophic niches, being both taxonomically and ecologically diverse. These features, combined with their high sensitivity to human-induced landscape changes (García-Morales et al. 2013), their local abundance and relative ease to sample qualifies them as a well-suited indicator group to examine the effects of anthropogenic environmental changes, including fragmentation, on tropical biota (Jones et al. 2009).

Although bats, and in particular the species-rich Phyllostomidae have been the chosen group for numerous fragmentation studies across the New World, generalisations about how Neotropical bats respond to fragmented landscapes are difficult (reviewed in Meyer et al. 2016). The difficulty in detecting consistent trends among bat responses to fragmentation may be at least partially explained by between site differences in bat assemblages, fragmentation history and the degree of contrast between the structure of the remaining forests fragments and the matrix in which they are embedded in (Meyer et al. 2016). Still, the available evidence seems to suggest that frugivorous and nectarivorous

bats tend to increase their abundance in fragmented landscapes due to additional food resources (Delaval and Charles-Dominique 2006; Bobrowiec and Gribel 2010; Farneda et al. 2015) whereas the abundance of gleaning animalivores tends to decrease in response to insufficient roosting and prey resources (Gorresen and Willig 2004; Meyer and Kalko 2008; Farneda et al. 2015).

Early research on the impacts of fragmentation on Neotropical bats was profoundly influenced by MacArthur and Wilson's (1967) island biogeography theory (IBT) and focused chiefly on the effects of patch area and isolation metrics, while ignoring the matrix in which fragments are embedded. Whereas population- and assemblage-level responses were found for both patch area (Cosson et al. 1999) and isolation (Estrada et al. 1993; Meyer and Kalko 2008) some studies found either weak or no influence of these metrics (e.g. Faria 2006; Pardini et al. 2009). Over the years the conceptual basis of fragmentation studies matured to reflect the importance of the matrix (Kupfer et al. 2006; Driscoll et al. 2013) and Neotropical bat-fragmentation studies came to integrate landscape features such as habitat composition and configuration. The effect of landscape context on Neotropical bats remains understudied but the available evidence suggests that similarly to many other taxa, landscape-scale habitat amount appears to have a stronger effect than fragmentation *per se* (Fahrig 2003). Accordingly, studies analysing land-bridge island systems have found forest cover at the landscape-scale to be a strong determinant of species richness and composition (Meyer and Kalko 2008; Henry et al. 2010). However, studies on non-aquatic matrix systems demonstrated a less marked response to forest amount and consistently, population- and assemblage-level responses to configuration were highly context-specific (Gorresen and Willig 2004; Klingbeil and Willig 2009, 2010; Cisneros et al. 2015). Detection of common responses between different studies is further complicated by findings that Neotropical bats respond to

landscape structure in a scale-sensitive manner (Pinto and Keitt 2008; Klingbeil and Willig 2009, 2010; Chambers et al. 2016).

As previously mentioned, edge effects are important drivers of assemblage dynamics in fragmented landscapes (Ewers and Didham 2006; Haddad et al. 2015). Yet, despite evidence that edge sensitivity is an important determinant of vulnerability to fragmentation in Neotropical bats (Meyer et al. 2008), studies targeting how bat assemblages react to the changes in biotic and abiotic conditions created by forest edges in the Neotropics are still scarce (Meyer et al. 2016). Nonetheless, the existing studies indicate that at the landscape-level, edges appear to influence species richness and assemblage composition in systems with aquatic matrices (Meyer and Kalko, 2008; Henry et al. 2010). However, responses in systems with less structurally contrasting matrices have been mixed, with some studies failing to detect any responses (Gorresen and Willig 2004; Klingbeil and Willig 2009, 2010), while others found evidence for an influence of forest edges (Bolívar-Cimé et al. 2013; Chambers et al. 2016; Arroyo-Rodríguez et al. 2016). This emphasizes the influence of level of fragment-matrix contrast on edge effects. The responses to edges were also found to be scale-dependent (Klingbeil and Willig 2009) and somewhat ensemble-specific, with gleaning animalivorous bats exhibiting more pronounced responses than frugivorous bats (Henry et al. 2010). These inconsistencies across spatial-scales, ensembles and matrix context, alongside the scarcity of studies addressing edge effects on Neotropical bats precludes a concise understanding of how New World bat communities are impacted by habitat edges.

While the spatial aspects of fragmentation upon Neotropical bats have received some research attention, the temporal dimension has been, up-to-now, overlooked (Meyer et al. 2016). Understanding of how communities respond to fragmentation over time is especially important in dynamic, non-aquatic matrix systems in which temporal

heterogeneity in matrix resources as well as structural changes alter matrix permeability and, consequently, fragment connectivity (Laurance et al. 2011). These changes in matrix permeability are particularly evident in regenerating landscapes, in which secondary regrowth is reclaiming previously deforested land (Chazdon 2014). As secondary forest matures not only the composition of the matrix is altered but edge contrast also changes, generally leading to temporal variation in the strength of edge effects (Laurance et al. 2007).

Across the Neotropics several studies have investigated the response of bat assemblages to different secondary forest age classes (e.g. Castro-Luna et al. 2007; Bobrowiec and Gribel 2010; Avila-Cabadilla et al. 2012). Despite being based on chronosequences in which space is used as a proxy for time and therefore incapable to fully disentangle the temporal from the spatial component (Dornelas et al. 2013), these studies have shown that the maturation of second growth vegetation increases matrix permeability for Neotropical bats, allowing species to recolonize forest remnants. However, although researchers have tackled how matrix dynamics over time mediates fragmentation responses in some taxa such as birds and beetles (Quintero and Roslin 2005; Stouffer et al. 2011), no study has investigated how matrix temporal heterogeneity affects bat assemblages in fragmented landscapes.

Bat research at the Biological Dynamics of Forest Fragments Project

Aware of the importance of baseline data, BDFFP researchers began data collection prior to fragment isolation in 1979. Unfortunately, bats were not included in these first sampled groups and the first bat studies were carried out more than 15 years after forest clearance, in the late-90s. The first bat studies at the BDFFP were led by Erica Sampaio (Sampaio et al. 2003, PhD dissertation) and Enrico Bernard (Bernard 2001, MSc dissertation). Whereas Sampaio's study sampled 6 continuous forest sites and 6 fragments (3 of 1 ha and 3 of 10 ha) with ground level mistnets and was focused on the impacts of forest fragmentation, Bernard's was restricted to continuous forest and used a combination of canopy- and ground-level mistnets to investigate the patterns of vertical stratification in BDFFP primary forests (Bernard 2001). Data collected by Enrico Bernard were also used to assess the diet, activity and reproduction of Central Amazonian bats (Bernard 2002). Soon after, a new research team used ground-level misnetting to investigate how secondary vegetation type influenced bat assemblages in the regenerating matrix (Bobrowiec and Gibrel 2010). More recently seed dispersal by bats was also studied but this time no mistnetting was conducted (Wieland et al. 2011).

Since 2011 and with the beginning of this study, which ran parallel to several other independent (but interrelated) bat research projects, the knowledge about the chiropteran fauna of the BDFFP and their responses to forest fragmentation has massively increased. Mist net data collected for this study was used for 5 MSc theses, focussing on vertical stratification of bat assemblages in continuous forest and forest fragments (Silva 2012), on matrix and area effects (Groenenberg 2012), on trait-related fragmentation vulnerability (Farneda 2013; Farneda et al. 2015), on seasonal responses to fragmentation (Ferreira 2014) and on the vertical stratification of aerial insectivorous bats in primary and secondary forests (Navarro et al. 2014). Additionally, parallel to this, two other

doctoral theses (one focusing on the impacts of forest fragmentation on aerial insectivorous bats (Adrià Lopez-Baucells) and another on bat functional diversity (Fábio Farneda)) are currently ongoing and the intensive fieldwork undertaken at the BDFFP during the last few years materialized into the first morphological and acoustic field guide for Central Amazonian bats (Lopéz-Baucells et al. 2016) and numerous natural history notes (e.g. Rocha et al. 2012; Lopéz-Baucells et al. 2013; Rocha and Lopéz-Baucells 2014; Lopéz-Baucells et al. 2014; Rocha et al. 2016).

Main aims and outline of the thesis

The general objective of this thesis was to explore both the spatial and temporal variation in responses to fragmentation within the BDFFP landscape, using bats as a model group. Based on extensive fieldwork undertaken at several sites in secondary forest, forest fragments and continuous forest between August 2011 and June 2014, I approach the following research topics, each representing an independent publication:

1. *"Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects"*
2. *"Does sex matter? Gender-specific responses to forest fragmentation in Neotropical bats"*
3. *"Design matters: an evaluation of the impact of small man-made forest clearings on tropical bats using a before-after-control-impact design"*
4. *"Neotropical bats in a recovering fragmented landscape: effects of secondary forest regrowth on specialist and generalist species"*

The specific objectives, main methodological approaches and key findings of each chapter are presented below.

Chapter 2. Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects

Habitat loss, fragmentation and degradation are central issues in biodiversity conservation. From their early roots in classical island biogeography theory, forest fragmentation studies have since matured to incorporate landscape ecological principles, with an emphasis on the spatial arrangement of fragments and on matrix composition. However, despite a vast literature on the topic, studies focusing on the full disturbance gradient of fragmented forest landscapes (continuous forest and fragment interiors, forest edges and matrix habitats) are scarce and habitat quality metrics are rarely considered.

In this study, we took advantage of the unique experimental setting provided by the BDFFP to investigate how tropical bat assemblages respond to vegetation structure and landscape-scale characteristics across an interior-edge-matrix disturbance gradient. Our analyses are based on more than 4000 captures of 50 species and we expand on traditional fragmentation studies by using a multi-scale approach to simultaneously investigate how different biodiversity metrics (species richness, evenness and abundance) are affected by local-scale vegetation structure and landscape-scale forest amount and fragmentation metrics at a range of different focal scales.

Despite the "soft" matrix in which the BDFFP fragments are embedded (composed of ≥ 16 year secondary vegetation) we found strong area-related effects and responses to local- and landscape-level attributes were scale-dependent and ensemble-specific. The findings of this study add to an increasing body of evidence suggesting that scale-sensitive measures of landscape structure are needed for a more comprehensive understanding of the effects of fragmentation on tropical biota.

Chapter 3. Does sex matter? Gender-specific responses to forest fragmentation in Neotropical bats

One of the major challenges of conservation is to understand how species can survive in fragmented landscapes. Yet, while many vertebrate groups are known to exhibit differences between sexes in habitat use, sex-specific responses to forest fragmentation remain little explored.

In this study, we investigated male and female responses of eight Neotropical bat species to an interior-edge-matrix disturbance gradient at the BDFFP. To account for seasonality effects we conducted analyses independently for the dry and wet seasons and, for the two most common species, we further investigated the responses to vegetation structure and landscape-scale composition and configuration at a range of different focal scales.

Our results unveiled that both sexes responded similarly to the interior-edge-matrix gradient. However, for three species, we found distinct differences in habitat use between male and female bats for at least one of the seasons. Male-female ratio was balanced in continuous forest and fragment interiors, however, for most species females outnumbered males at edge and matrix sites. Abundance responses to vegetation structure and landscape-scale composition and configuration differed between male and female bats of the two most common species. The observed differences between the responses of male and female bats were consistently more pronounced in dry season. The findings of this study unveil considerable differences in the response of male and female bats to tropical forest disruption and degradation and suggest that future studies investigating the effects of habitat modification on tropical forest vertebrate communities should consider both sexes, due to the possibility that sex-specific differences in habitat use exist.

Chapter 4. Design matters: an evaluation of the impact of small man-made forest clearings on tropical bats using a before-after-control-impact design

Across the tropics, widespread human disturbances are moulding human-modified landscapes in which small (< 100 m wide) man-made forest clearing are conspicuous features. Since many old-growth specialists avoid even narrow (< 30 m wide) clearings, understanding the impacts of these small-scale disturbances on primary forest species is paramount to frame effective conservation strategies. In this study, we used a periodical re-isolation of the fragments at the BDFFP, as a before-after-control-impact experiment to investigate the short-term consequences of small clearings on the occupancy of Neotropical bat assemblages in fragment interior, edge and matrix habitats. For this, we sampled interior, edge and matrix sites of eight forest fragments and six control sites in continuous forest before and after the experimental manipulation, capturing ~6 000 bats.

We observed a decline in species richness in all habitats other than fragment edges after fragment re-isolation. Although responses were idiosyncratic, the decline in species richness was more pronounced for forest specialist than for generalist species. Moreover, the similarity between assemblages in continuous forest and fragment interiors, edges and matrix was smaller after fragment re-isolation than before the experimental manipulation. Sampling of experimental controls (sites in continuous forest) both before and after the re-isolation of the fragments unveiled that much of the variation in bat species occupancy between sampling periods did not arise from fragment re-isolation but rather reflected natural spatiotemporal variability. This highlights the need to sample experimental controls both before and after disturbance occurs and suggests caution in the interpretation of results from studies in which the impacts of habitat modification are investigated based uniquely on data collected using space-for-time substitution approaches.

Chapter 5. Neotropical bats in a recovering fragmented landscape: effects of secondary forest regrowth on specialist and generalist species

Secondary forests are now the largest forest cover type across the humid tropics and although the potential of secondary forests to conserve tropical biodiversity remains hotly debated, mounting evidence suggests that secondary forest regrowth can lessen fragmentation impacts in modified landscapes. In this chapter, we investigated how bat assemblages at the BDFFP were influenced by the regeneration of the matrix vegetation from the late-90s to 2011-2013. For this, we compared the occupancy and abundance of generalist and specialist bat species in continuous forest, forest fragments and secondary forest, ~15 and ~30 years after the initial forest clearance.

We show that whereas generalist species were not favoured by secondary forest regeneration in the matrix, specialist species greatly benefited from secondary forest maturation. Species responses were idiosyncratic and assemblage similarity between continuous and modified habitats (fragments and secondary forest) did not increase with regeneration time. Our results show that the potential of secondary forests for reverting faunal declines in fragmented tropical landscapes increases with secondary forest age and that old-growth specialists, which are often of most conservation concern, are the greatest beneficiaries from secondary forest maturation. Although conservation of old-growth forest should always be prioritized, the findings of this study support claims that the protection of old (> 20 years) secondary forests should be incentivized as it brings considerable net benefits to global tropical conservation efforts.

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CHAPTER 2

Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects

Rocha, R., López-Baucells, A., Farneda, F.Z., Groenenberg, M., Bobrowiec, P.E., Cabeza, M., Palmeirim, J.M. and Meyer, C.F., 2016. *Landspcae Ecology*, DOI: 10.1007/s10980-016-0425-3

CHAPTER 2

Consequences of a large-scale fragmentation experiment for Neotropical bats: disentangling the relative importance of local and landscape-scale effects

Abstract

Context Habitat loss, fragmentation and degradation are widespread drivers of biodiversity decline. Understanding how habitat quality interacts with landscape context, and how they jointly affect species in human-modified landscapes, is of great importance for informing conservation and management.

Objectives We used a whole-ecosystem manipulation experiment in the Brazilian Amazon to investigate the relative roles of local and landscape attributes in affecting bat assemblages at an interior-edge-matrix disturbance gradient.

Methods We surveyed bats in 39 sites, comprising continuous forest, fragments, forest edges and intervening secondary regrowth. For each site, we assessed vegetation structure (local-scale variable) and, for five focal scales, quantified habitat amount and four landscape configuration metrics.

Results Smaller fragments, edges and regrowth sites had fewer species and higher levels of dominance than continuous forest. Regardless of the landscape scale analysed, species richness and evenness were mostly related to the amount of forest cover. Vegetation structure and configurational metrics were important predictors of abundance, whereby the magnitude and direction of response to configurational metrics were scale-dependent. Responses were ensemble-specific with local-scale vegetation structure being more important for frugivorous than for gleaning animalivorous bats.

Conclusions Our study indicates that scale-sensitive measures of landscape structure are needed for a more comprehensive understanding of the effects of fragmentation on tropical biota. Although forest fragments and regrowth habitats can be of conservation significance for tropical bats our results further emphasize that primary forest is of irreplaceable value, underlining that their conservation can only be achieved by the preservation of large expanses of pristine habitat.

Keywords Amazon; edge effects; FRAGSTATS; landscape context; matrix; secondary forest; spatial scale; vegetation structure.

Introduction

Anthropogenic forest loss and fragmentation are key drivers of the ongoing defaunation crisis (Dirzo et al 2014). This erosion of biological diversity has repeatedly been associated with human population growth and rising per-capita consumption (Laurance et al 2014) whose future increases are expected to be greatest in the tropics where much of the planet's biodiversity resides (Bradshaw et al 2008; Gibson et al 2011).

In human-modified landscapes, habitat loss and fragmentation typically co-occur with habitat degradation (Fischer and Lindenmayer 2007). Deterioration in habitat quality is most noteworthy near primary forest edges and in regenerating forests, where biotic and abiotic gradients and alternative successional pathways lead to marked differences in vegetation structure (Williamson et al 2014; Faria et al 2009). Forest edges and regenerating forests are ubiquitous features of tropical landscapes (Chazdon 2014). For instance, ~32000 km of new forest edges are created annually in the Brazilian Amazon by deforestation alone (Broadbent et al 2008) and, in 2000, ~140 x 10^3 km^2 of the region's

land area was composed of regenerating forests (Carreiras et al 2006). Regenerating secondary forests profoundly influence the spatio-temporal distribution of many species (e.g. Barlow et al 2007; Banks-Leite et al 2010). However, studies focussing on the full disturbance gradient of continuous forest (CF) and fragment interiors (I), forest edges (E) and matrix (M) habitats (hereafter IEM gradients) in fragmented landscapes are scarce, and habitat quality metrics are rarely incorporated into landscape-scale fragmentation studies (Galitsky and Lawler 2015). This translates into a poor understanding of how habitat quality interacts with landscape context and how they jointly affect species persistence and abundance in human-modified landscapes.

Bats comprise a large fraction of tropical mammalian fauna and play key ecological roles in pollination, seed dispersal and insect suppression (Kunz et al 2011). They are acutely sensitive to human-induced landscape changes (García-Morales et al 2013; Meyer et al 2016) and their local abundance and diversity qualifies them as a well-suited indicator group to examine the effects of fragmentation on tropical biota (Jones et al 2009).

MacArthur and Wilson's (1967) island biogeographic theory profoundly influenced early research on fragmented ecosystems. Studies on tropical bats were no exception to this, with earlier work focusing mainly on the effects of patch area and isolation metrics (Cosson et al 1999; Schulze et al 2000). As the conceptual basis of fragmentation studies matured, landscape characteristics such as habitat amount and configuration came to be recognized as important determinants of bat species persistence in modified forest landscapes and the few studies that have explored tropical bat associations with landscape structure at multiple spatial scales have found assemblages to respond in a scale-sensitive manner (reviewed in Meyer et al 2016). This scale sensitivity in bat responses towards landscape structure likely reflects interspecific

differences in species ecological traits such as diet, body size and home range which are linked to the scale at which individual species perceive and interact with their environment (Pinto and Keitt 2008; Meyer et al 2016). Scale dependency is also indicative of the influence of smaller scale drivers upon ecological processes that operate at larger spatial scales (McGill 2010). By imposing limitations on mobility and food detection, microhabitat characteristics such as vegetation structure strongly influence the type and number of bat species co-occurring on a local scale (Marciente et al 2015). However, vegetation structure is rarely included in multi-scale fragmentation studies although it has been suggested to constitute a better predictor of the activity of forest-dwelling bats than landscape-level features (Erickson and West 2003; Charbonnier et al 2016) and is likely to modulate ecological responses to fragmentation at the landscape level.

The Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon is the world's largest and longest-running experimental study of forest fragmentation (Laurance et al 2011). Vertebrate assemblages at the BDFFP have been found to be sensitive to fragment size (Ferraz et al 2007; Boyle and Smith 2010), edge effects (Lenz et al 2014; Powell et al 2015), matrix composition (Antongiovanni and Metzger 2005; Bobrowiec and Gribel 2010), local vegetation structure (Stratford and Stouffer 2013; Mokross et al 2014) and landscape-scale characteristics (Stouffer et al 2006; Boyle and Smith 2010). However, no study has jointly investigated how vegetation structure and landscape composition and configuration affect the occurrence and abundance patterns of its vertebrate assemblages. Here we address this gap by examining how BDFFP bat assemblages respond to an IEM disturbance gradient in a landscape where fragments are embedded in a "soft" matrix composed of advanced secondary vegetation. Specifically, we address the following questions:

(1) How do bat species richness, evenness, abundance and assemblage composition change along IEM (interior, edge and matrix) and size (CF, 100, 10 and 1 ha fragments) gradients? Relative to CF interiors we expected forest fragments to exhibit reduced species richness and evenness and we hypothesized that differences in response metrics (species richness, evenness, abundance and assemblage composition) between IEM habitats would decrease with fragment size. Additionally, we predicted frugivores to be more edge- and matrix-tolerant than gleaning animalivorous bats.

(2) What is the relative importance of local vegetation structure versus landscape-scale primary forest cover and configuration as determinants of bat species richness, evenness and abundance? And how does it vary across multiple spatial scales? We anticipated different response metrics to relate differently to vegetation structure and landscape characteristics and predicted that responses would be scale-dependent with all three assemblage attributes (species richness, evenness and abundance) responding predominantly to forest cover. We also expected gleaning animalivores to present stronger negative effects towards configuration metrics than frugivorous bats.

Material and methods

Study area and site selection

Fieldwork was conducted at the BDFFP, located ~80 km north of Manaus (2°30'S, 60°W), Brazil (see Fig. S1 in the supplementary material). The area is classified as tropical moist forest, and is characterized by a mosaic of *terra firme* rainforest, secondary regrowth, and primary forest fragments. Annual rainfall varies from 1900-3500 mm, with a dry season between June and October (Laurance et al 2011). The forest fragments were isolated from continuous forest by distances of 80-650 m in the early 1980s, and are

categorized into size classes of 1, 10 and 100 ha. Each fragment was re-isolated on 3-4 occasions prior to this study, most recently between 1999 and 2001 (Laurance et al 2011). The matrix is composed of tall secondary forest dominated mainly by *Vismia* spp. and *Cecropia* spp. (Mesquita et al 2001).

Bats were sampled in eight forest fragments - three of 1 ha, three of 10 ha and two of 100 ha (Colosso, Porto Alegre and Dimona camps) - and nine control sites in three areas of CF (Cabo Frio, Florestal and Km 41 camps) (Fig. S1). Sampling was conducted in the interiors and at the edges of all eight fragments, as well as at eight sites located in the nearby secondary regrowth, 100 m away from the edge of each fragment. A similar sampling scheme was employed for CF, with nine sampling sites in the interior, three at the edge, and three matrix sites located 100 m away from the forest edge. Therefore, a total of 39 sites were sampled. Distances between interior and edge sites of CF and fragments were respectively 1118 ± 488 and 245 ± 208 m (mean ± SD).

Bat surveys

Each sampling site was visited eight times over a 2-year period, between August 2011 and June 2013. Bats were captured using 14 ground-level mist nets (12 x 2.5 m, 16 mm mesh, ECOTONE, Poland) in CF and fragment interiors, and seven ground-level mist nets at the edge and matrix sites. Mist nets were deployed along existing trails which are known to be used by Neotropical bats as commuting flyways (Palmeirim and Etheridge 1985). At edge sites, these trails ran parallel to the border between primary forest and secondary regrowth. In our study area mist netting efficiency was found to be highest in the first few hours after sunset (Bernard 2002). Sampling therefore started at dusk and was performed for six hours during which nets were visited at intervals of ~20 minutes. Mist netting at the same location for consecutive days can lead to diminishing

capture efficiency over time (Marques et al. 2013). Such net-shyness related bias was avoided by spacing visits to the same site three to four weeks apart. Species were identified following Gardner (2007) and Lim and Engstrom (2001), and taxonomy follows Gardner (2007). Most adult bats were marked with individually numbered ball-chain necklaces (frugivores and *Pteronotus parnellii*) or subcutaneous transponders (gleaning animalivores). We restricted analyses to phyllostomids and *P. parnellii*, since all other species in Neotropical bat assemblages are known to be inadequately sampled with mist-nets (Kalko 1998).

Influence of fragment-size and interior-edge-matrix gradient

Species richness, evenness and abundance

Differences in species richness, evenness, and abundance between size- (CF, 100, 10 and 1 ha fragments) and IEM-gradients were assessed using generalized linear mixed-effects models (GLMMs), fitted in the R package "*lme4*" (Bates 2010). A categorical variable combining information of both the size- and IEM-gradient was specified as a fixed effect, and a random term nesting "site" within "location" (the latter referring to the six research camps; Fig. S1) was incorporated. This approach accounts for potential autocorrelation between sites within the same location (Bolker et al 2009). For each size category and IEM, species richness and evenness, the latter quantified as Hurlbert's probability of interspecific encounter (PIE), were computed using rarefaction. Rarefaction was performed using EcoSim software v.7 (Gotelli and Entsminger 2004) based on 1000 random rearrangements and independent sampling of individuals, rarefying to the abundance level of the site with the lowest number of captures. Total number of captures per site was used to compare differences in abundance using a Poisson GLMM, with the

site's total number of mist-net hours (1 mist-net hour [mnh] equals one 12-m net open for 1 h) specified as an offset. High inter-fragment variation in capture rates precluded robust inference about how fragment size affects capture rates.

Differences in abundance between size- and IEM-gradients were therefore analysed by both considering the distinct fragment size categories (100, 10 and 1 ha fragments) independently and by lumping the capture data from all fragments. Significant effects were further evaluated via multiple comparison tests with Tukey contrasts (adjusted *P*-values reported) using the R package "*multcomp*" (Hothorn et al 2013).

Assemblage composition

Differences in assemblage composition were characterized by means of a non-metric multidimensional scaling (NMDS) ordination based on a Bray-Curtis dissimilarity matrix, using the number of captures standardized by the site's effort (bats per mnh) and scaled to a mean of 0 and standard deviation of 1. Compositional differences between size- and IEM-gradient habitat types were evaluated with a permutational multivariate analysis of variance (PERMANOVA). Both analyses were conducted using the *"vegan"* package in R (Oksanen et al 2013).

Ensemble-specific responses

According to available literature (Bernard 2001, 2002; Giannini and Kalko, 2004; Ramos Pereira et al 2010) species were grouped into frugivores (subdivided into shrub and canopy frugivores), gleaning animalivores, aerial insectivores and nectarivores (Table S1). The same approach used to compare total abundance was used to explore ensemble-specific differences in abundance across the size- and IEM-gradients.

Influence of local and landscape-scale variables

Vegetation structure

Vegetation structure was characterized within three 100 m^2 (5 x 20 m) plots established 5 m from each side of the mist net transects. In each plot, nine variables were quantified: (i) number of trees (diameter at breast height [DBH] ≥ 10 cm), (ii) number of woody stems (DBH < 10 cm), (iii) average DBH of trees ≥ 10 cm, (iv) percent canopy cover (estimated as the average of four spherical densiometer readings), (v) number of palms, (vi) number of *Vismia* spp. and *Cecropia* spp. (the fruits of both genera are consumed by several frugivorous bat species, e.g. Bernard 2002; Giannini and Kalko 2004), (vii) liana density (visually classified every 5 m in five categories varying from no lianas to very high liana density), (viii) tree height (based on visual estimates of 25 trees ≥ 10 cm DBH) and (ix) vertical foliage density (calculated as the sum of the values obtained by visual estimation at seven height intervals [0-1 m, 1-2 m, 2-4 m, 4-8 m, 8-16 m, 16-24 m, 24-32 m] using 6 categorical classes [0 = no foliage, 1 = very sparse 0-20%, 2 = sparse 20-40%, 3 = medium 40-60%, 4 = dense 60-80%, 5 = very dense 80-100%]).Values for each sampling site were calculated as the average across replicated plots (Table S2).

Vegetation variables were log(x + 1) transformed, standardized to a mean of zero and a standard deviation of one, and submitted to a Principal Components Analysis (PCA). The scores of the first axis (PCA1) were then used as predictor variable summarizing vegetation structure (Fig. S2 and Table S3) in modelling bat responses to local habitat and landscape structure.

Landscape structure

To quantify compositional and configurational aspects of landscape structure we used a detailed forest vs non-forest map of the BDFFP landscape based on 2004 LandSat Thematic Mapper (TM) satellite images (30 m spatial resolution). Land cover classification was obtained through supervised classification (bands 7, 5, 4, 3, 2 and 1), with thorough field checking performed to validate map accuracy. Primary forest (hereafter simply "forest") was clearly distinguished from second growth. Landscape metrics were chosen based on their reported influence on Neotropical bats (Gorresen and Willig 2004; Meyer and Kalko 2008; Klingbeil and Willig 2009; Avila-Cabadilla et al 2012) and were calculated using Fragstats v.4.1 (McGarigal et al 2012) for buffers with radii of 250, 500, 750, 1000 and 1500 m around each of the 39 sampling points. Buffer scales were selected so as to encompass the home ranges of different-sized bat species while at the same time minimizing spatial overlap between neighboring sites (Meyer et al 2008). Five metrics were selected to represent: (a) habitat amount (forest cover) and (b) habitat configuration (mean patch area, patch density, edge density and mean shape index).

Relative importance of local and landscape-scale predictors of bat responses

The relative importance of local (vegetation structure) vs landscape-scale characteristics in determining species richness, evenness and abundance were investigated at the five different focal scales using GLMMs. For this, we used rarefied species richness, evenness and total number of captures at each site as response variables. Additionally, GLMMs using total number of captures per site of frugivores and gleaning animalivores, respectively, were used to explore ensemble-specific relationships. Low

number of captures precluded separate analyses for the other ensembles. Severe collinearity between predictor variables can undermine statistical inference in GLMMs (Dormann et al 2013). We therefore quantified collinearity by calculating each predictor's variance inflation factor (VIF) within a set of predictors that always included vegetation structure and habitat amount (forest cover). As VIFs > 10 are known to indicate ''severe'' collinearity (Neter et al 1990) we reduced our set of predictor variables (by excluding mean patch area and mean shape index) so that those included in the final set presented a VIF < 6 in all analysed buffers.

Analyses were restricted to a subset of a priori selected models comprising plausible combinations of local (vegetation structure) and landscape predictors (forest cover, edge density and patch density). For each response variable and landscape-scale separate sets of models were defined, which considered (i) each metric independently, (ii) vegetation structure and each landscape metric independently, (iii) vegetation structure and habitat configuration metrics, (iv) forest cover and each habitat configuration metric independently and (v) configuration metrics only. Each model included a random term accounting for the nested sampling design (site within location). Model goodness-of-fit was assessed as the marginal R^2_m and conditional R^2_c (Nakagawa and Schielzeth 2013). Following Burnham and Anderson (2002), the most parsimonious models were selected using Akaike's Information Criterion corrected for small samples sizes (AIC_c). Model-averaging was used to obtain parameter estimates for the models with an AIC_c difference from the best model (Δ_i) < 2 (Burnham and Anderson 2002). Residual spatial autocorrelation in the best-fit GLMMs was inspected by means of Moran's *I* test. For these best-fit models, the variation independently explained by each explanatory variable was then determined by hierarchical partitioning analysis using the "*hier.part*" package (Walsh and Mac Nally 2013), modified to accommodate a model offset [log(effort)] for

abundance data (Jeppsson et al 2010). Following Benchimol and Peres (2015), hierarchical partitioning was conducted only considering fixed effects. Unless otherwise stated, all analyses were conducted in R v3.0.2 (R Development Core Team 2013).

Results

During 18650 mnh we captured 4210 bats belonging to six families and 55 species (Table S1). Phyllostomids and mormoopids (*P. parnellii*) were the dominant groups, accounting respectively for 90.9% (3827) and 6.5% (272) of total captures.

Responses to size- and interior-edge-matrix gradients

Species richness, evenness and abundance

Species richness was significantly higher in CF interiors than in any fragment size class, with the exception of the 100 ha fragment interiors (Fig. 1). Similarly, edge and matrix sites adjoining CF were more species-rich than those adjacent to fragments and, for both interior and matrix habitats, species richness tended to increase with fragment size. Conversely, this pattern did not hold for edge habitats as the edges of the 1 ha fragments were surprisingly diverse, attaining comparable richness to those of CF (Table S4 in Online Supplementary Material).

Evenness showed a similar pattern to species richness, with all habitats other than the 100 ha fragment interiors and CF edges being significantly less even than CF interiors (Table S4 in Online Supplementary Material). Evenness was higher for edge and matrix habitats adjoining CF and 100 ha fragments, and again, the edges of 1 ha fragments had significantly higher evenness than those of the other size classes.

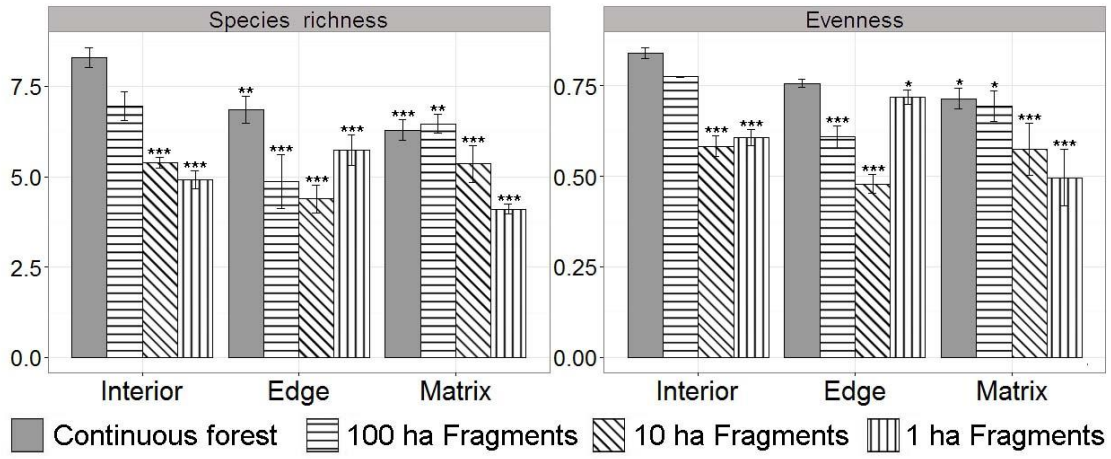

Fig. 1 Comparison of rarefied species richness and evenness (mean ± SE) across the interior-edge-matrix as well as fragment-size gradient. Asterisks denote significant differences relative to continuous forest interiors (*** P < 0.001; ** P < 0.01; * P < 0.05).

For both CF and fragments, total species abundance increased progressively from interior to edge and matrix habitats, with capture rates in the edge and matrix habitats being significantly higher than in CF interiors. However, when the most common species (*Carollia perspicillata*) was excluded, the effect only remained significant for the comparison with CF edges (Fig. 2; Table S5 in Online Supplementary Material; see Fig. S3 for results by fragment size).

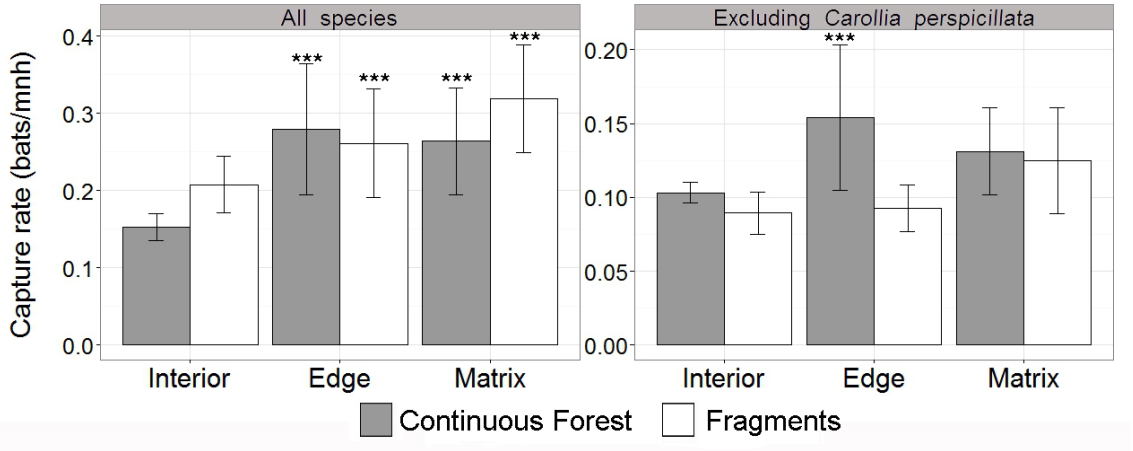

Fig. 2 Mean (± SE) capture rate (bats/mnh) for interior, edge and matrix sites of continuous forest and forest fragments. Asterisks denote significant differences relative to continuous forest interiors (*** P < 0.001).

Assemblage composition

The NMDS ordination had a stress value of 0.095, conveying a good representation of the data along two dimensions. Bat assemblage composition differed significantly across the size- and IEM-gradients (Fig. 3; F_{11} = 2.316, R^2 = 0.486, P = 0.001). The interiors of each fragment size category formed a distinct cluster and the 100 ha fragment interiors grouped closely to the cluster formed by CF interiors, indicating high assemblage similarity. Edge and matrix sites clustered independently from CF and 100 ha fragment interiors and presented a large spread along the first ordination axis.

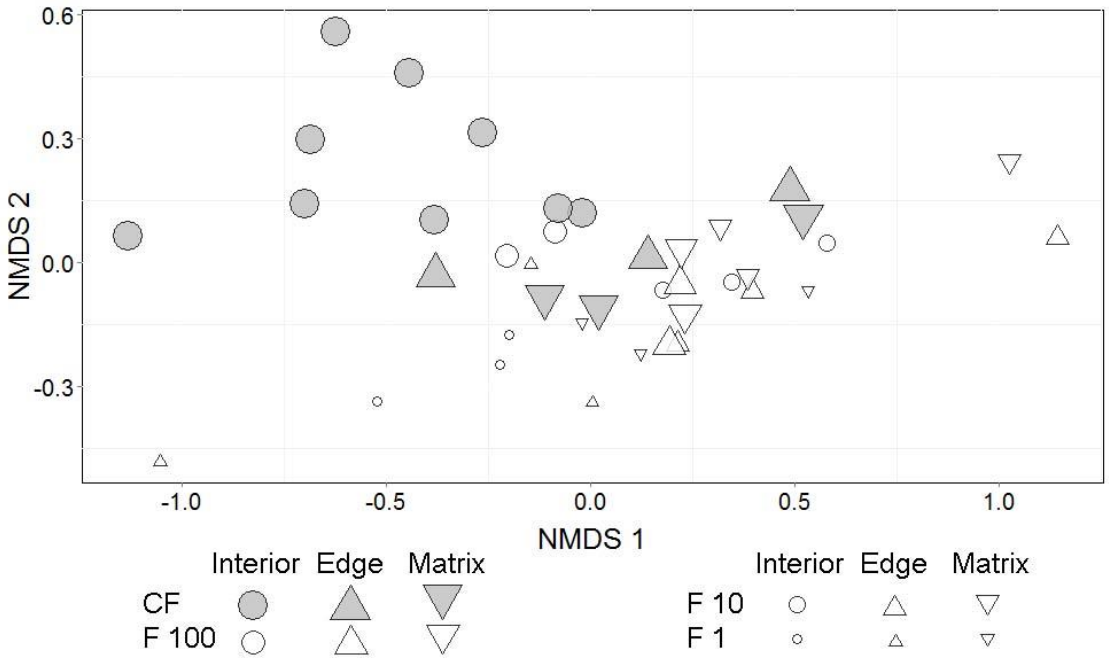

Fig. 3 Arrangement of the 39 sampling sites along the axes of a nonmetric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity.

Ensemble-specific responses

Shrub frugivores was the ensemble with the most captures (69%), followed by gleaning animalivores with 12.5%. Shrub and canopy frugivores showed similar patterns of relative abundance, with higher capture rates in edge and matrix habitats compared to habitat interiors (Fig. 4; see Table S6 for results by fragment size). Capture rates for all frugivores and shrub frugivores were significantly lower at CF interiors than in any other habitat category. For canopy frugivores there was no significant difference between CF interiors and CF edges and fragment interiors. Conversely, compared with the same IEM habitat type, gleaning animalivores in fragments had significantly lower capture rates than in CF. The capture rate of aerial insectivores (*P. parnellii*) was lower in fragment interior, edge and matrix habitats than in CF interiors, and the abundance of nectarivores peaked in fragment interiors and CF edges. However, none of these differences were significant (Table S7 in Online Supplementary Material).

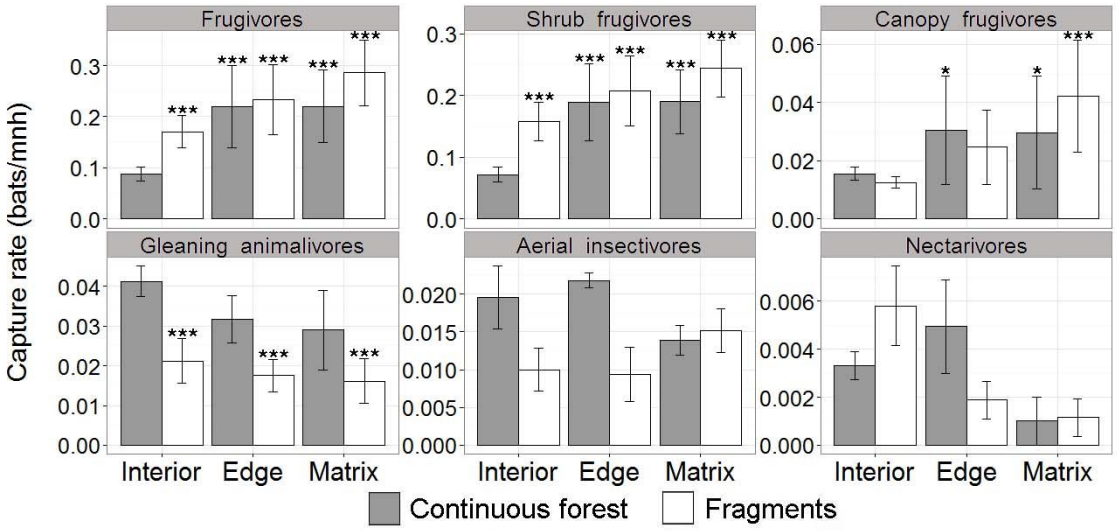

Fig. 4 Mean (± SE) capture rate (bats/mnh) for total frugivores, shrub frugivores, canopy frugivores, gleaning animalivores, aerial insectivores (*Pteronotus parnellii*) and nectarivores for the interior, edge and matrix habitats of continuous forest and forest fragments. Asterisks denote significant differences relative to continuous forest interiors (*** $P < 0.001$; * $P < 0.05$).

Influence of local and landscape-scale variables

Assemblage and ensemble associations with local and landscape metrics were scale-sensitive and varied according to the response variable analysed (Fig. 5 and 6). However, for most response metrics and spatial scales, relatively high model selection uncertainty made it difficult to unequivocally pinpoint either local vegetation structure or landscape-scale attributes as best predictors (Tables S8, S9 in Online Supplementary Material). GLMM residuals were not significantly spatially autocorrelated for evenness or any of the abundance models (Moran's I from -0.23 to 0.02, $P > 0.05$). However, for species richness and at the smallest spatial scale (250 m), one of the models included in the most parsimonious set ($\Delta AIC_c < 2$) presented spatially structured residuals (Moran's $I = -0.23$, $P < 0.05$) (Table S10 in Online Supplementary Material). Consequently, for this scale and response variable the results should be interpreted with caution as autocorrelation may prompt to an elevated Type I error.

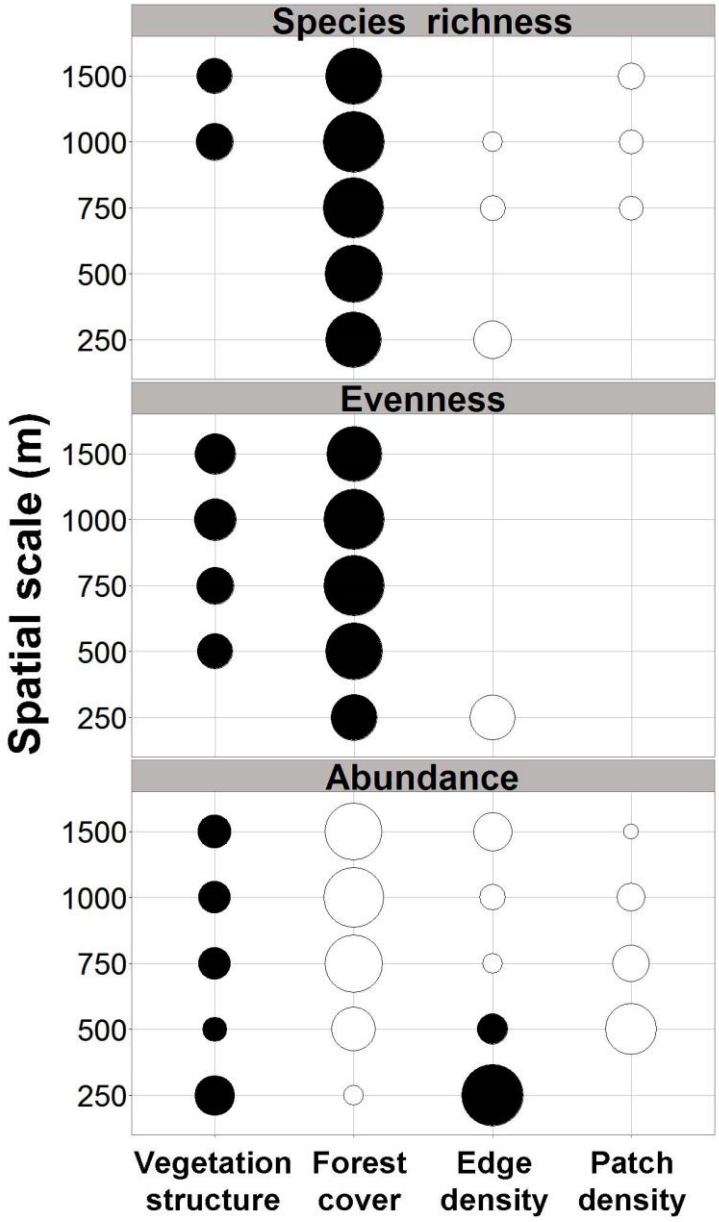

Fig. 5 Summary results of model averaging of the most parsimonious generalized linear mixed models (Akaike differences < 2 from the best model) investigating the relationship between local and landscape-scale attributes and various response metrics (species richness, evenness and total abundance) at five focal scales across the BDFFP, Central Amazon, Brazil. Symbol size is proportional to the variation explained by the respective predictor variable based on hierarchical partitioning and colour denotes the direction of the relationship: black = positive, white = negative. See Tables S8 and S9 in Online Supplementary Material for additional modelling results.

Vegetation structure, as represented by PCA1, was a particularly relevant predictor of total abundance and abundance of frugivores. Other than for the smallest (250, 500 and 750 m) spatial scales, with species richness and the abundance of gleaning animalivores as response variables and for the smallest spatial scale for evenness, vegetation structure was always included in the most parsimonious models. The PCA1 explained 42.02% of the total variance and represented a gradient from simpler vegetation structural complexity, typical of secondary forest (higher density of pioneer trees [*Vismia* spp. and *Cecropia* spp.] and woody stems [DBH <10 cm]; negative values), to higher structural complexity, typical of primary forest sites (more closed canopy cover and higher density of trees [DBH >10]; positive values) (Fig. S2 and Table S2). Its relationship was positive with respect to all response metrics analysed, indicating that more complex sites in terms of vegetation structure presented higher species richness, evenness and abundance. Forest cover emerged as the most important predictor of species richness and evenness, being positively associated with both and with the abundance of gleaning animalivores. Its influence on total and frugivore abundance was negative across all scales. The effect of edge density was particularly sensitive to scale, being positively correlated with total abundance and abundance of frugivores and gleaning animalivores at the smallest scales (≤ 500 m) and negatively at larger spatial scales. Lastly, patch density showed greater consistency as predictor across scales, being negatively associated with species richness, total abundance and, except at one spatial scale, with the abundance of frugivores and gleaning animalivores.

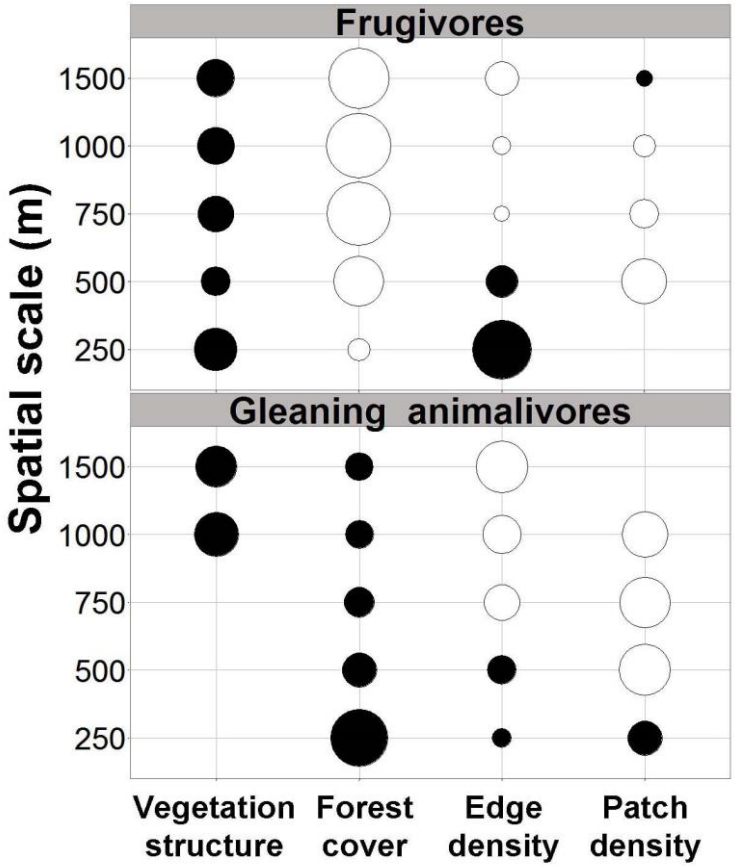

Fig. 6 Summary results of model averaging of the most parsimonious generalized linear mixed models (Akaike differences < 2 from the best model) investigating the relationship between local and landscape-scale attributes and the abundance of frugivores and gleaning animalivores at five focal scales across the BDFFP, Central Amazon, Brazil. Symbol size is proportional to the variation explained by the respective predictor variable based on hierarchical partitioning and colour denotes the direction of the relationship: black = positive, white = negative. See Tables S8 and S9 in Online Supplementary Material for additional modelling results.

Discussion

Our analyses revealed that patterns of bat species richness, evenness and abundance varied across the BDFFP landscape, and were affected by local- and landscape-level habitat attributes in a scale-dependent and ensemble-specific manner. This despite the low structural contrast between CF, forest fragments and surrounding secondary regrowth.

Responses to size- and interior-edge-matrix gradients

Compared with CF, smaller (≤ 10 ha) fragments harboured fewer species and their assemblages were characterized by higher levels of dominance, results consistent with previous studies addressing the impacts of fragmentation on tropical bats (Cosson et al 1999; Meyer and Kalko 2008; Struebig et al 2008; Estrada-Villegas et al 2010) and other taxa at the BDFFP (Laurance et al 2006b; Ferraz et al 2007; Boyle and Smith 2010) as well as elsewhere in the tropics (Benchimol and Venticinque 2014; Bregman et al 2014). These differences, though remarkable given the low fragment-matrix contrast at the time of our study and the relatively short distance between forest fragments and nearby CF, seem to result from the strong effect of trait-mediated environmental filters that selectively benefit bat species with reduced body mass and a phytophagous diet (Farneda et al 2015). This is likely attributable to the elevated abundance of pioneer plants in early successional habitats, which benefit many small-bodied nectarivorous and frugivorous phyllostomids (e.g., *Glossophaga* spp., *Carollia* spp., *Sturnira* spp.), but fail to provide enough food resources to fulfil the energetic requirements of larger species and those of higher trophic levels.

For both CF and forest fragments, edge habitats had fewer species and higher levels of dominance. These differences were more noticeable in larger fragments (100 ha) and CF, suggesting an area effect on the magnitude of contrast between interior and edge assemblages. Edge effects have long been identified as having major impacts on species distributions and dynamics (Ewers and Didham 2006). In the BDFFP fragments, edge effects are predominant drivers of ecological change (Laurance et al 2011), affecting vegetation structure (Didham and Lawton 1999) and acting synergistically with area effects (Laurance et al 2006a).

Neotropical bats are known to respond to habitat edges (Gorresen and Willig 2004; Meyer and Kalko 2008; Klingbeil and Willig 2009; Klingbeil and Willig 2010; Bolívar-Cimé et al 2013) and the few studies that have compared phyllostomid assemblages at the interiors and edges of fragments have reported declines in species richness (Faria 2006; Meyer and Kalko 2008). This pattern might result from the avoidance of these habitats by gleaning animalivorous bats, an ensemble identified as edge-sensitive in both high- (Meyer et al 2008) and low-contrast systems (Faria 2006). The underlying drivers of the higher edge-sensitivity exhibited by this ensemble remain to be tested but they might relate to changes in the densities of preferred arthropod prey or to restrictions to flight maneuverability imposed by denser understory vegetation near edges.

Although the most conspicuous edge effects at the BDFFP have been detected within 100 m of forest edges (Laurance et al 2002), results from French Guiana indicate that edge-mediated changes in bat assemblage structure may be noticeable as far as 3 km from the forest edge (Delaval and Charles-Dominique 2006). This suggests that even our CF interior sites (located on average more than 1 km away from the forest edge) are likely

to suffer from the effects of edge penetration and consequently their bat assemblages may reflect the influence of the modified secondary forest matrix.

Bat assemblages in secondary regrowth adjoining CF and 100 ha fragments were also richer and more even than assemblages adjacent to smaller fragments, suggesting a spillover of species from the more diverse CF and 100 ha fragment interiors into the matrix. Low-contrast matrix habitats are known to harbour diverse bat assemblages, both at the BDFFP (Bobrowiec and Gribel 2010) and elsewhere in the Neotropics (Avila-Cabadilla et al 2009; Avila-Cabadilla et al 2014; Mendenhall et al 2014). Our results indicate not only that matrix habitats influence fragment ecology at the BDFFP (Gascon et al 1999; Laurance et al 2011) but that the influence is bidirectional and that, similarly to birds (Powell et al 2013), bat species dependent on old-growth stands may exploit the nearby secondary regrowth for feeding or as flyways between food patches.

Human-induced habitat changes, including fragmentation, act as non-random filters selecting those species with the best combination of traits to survive in modified ecosystems (Smart et al 2006). In the humid Neotropics, capture rates of frugivores generally increase in fragmented or disturbed areas, whereas gleaning animalivores tend to decline, if not disappear, in modified habitats (Meyer et al 2016). Our results are consistent with this pattern. The *Vismia*- and *Cecropia*-dominated secondary vegetation that surrounds the fragments in our study landscape provides additional food resources that augments the abundance of frugivores such as *C. perspicillata* (Bobrowiec and Gribel 2010). However, regrowth habitats and forest fragments are structurally less complex than CF, and constitute less suitable habitat conditions for most gleaning animalivores due to insufficient roosting and prey resources (Gorresen and Willig 2004; Meyer and Kalko 2008). Nectarivorous bats have been documented to remain stable or increase in forest remnants and edge habitats, owing to elevated densities of food resources following

forest clearance and subsequent succession (García-Morales et al 2013; Meyer et al 2016; Chambers et al 2016). At the BDFFP, both nectarivorous birds (Stouffer et al 2006) and bats follow this pattern, adding to the evidence that nectar-feeders, together with frugivores, are the most resilient ensembles to habitat modification.

Influence of local and landscape-scale variables

Our data suggest that both local and landscape metrics are important in explaining the effects of fragmentation on tropical bat assemblages. At the local-scale, we observed that sites that are more similar to CF in terms of vegetation structure are able to support assemblages that are richer, more even and comprised of greater abundances of both frugivorous and gleaning animalivorous bats. These results agree with several other studies on aerial and terrestrial forest-dependent tropical vertebrates in modified landscapes (e.g. Benchimol and Venticinque 2014; Rocha et al 2015). However, they contrast with the findings from a study of bat assemblages in a land-bridge island system in Panama (Meyer and Kalko 2008), which provided little evidence for an effect of vegetation structure on bat species richness and assemblage composition. This may reflect the wider environmental gradient of our study (which encompassed CF and fragment interiors, edges and matrix habitats) in relation to the one analysed in Panama (limited to CF and fragment interiors and CF edges). Vegetation structure may therefore be a stronger determinant of assemblage diversity and composition in systems with high vegetation heterogeneity such as the ones comprising present-day agricultural and countryside ecosystems.

Across taxa, habitat loss has consistently been found to have a strong negative impact on species persistence whereas the effects of habitat fragmentation per se appear

to be weaker and more variable, both in terms of magnitude and direction (Fahrig 2013). This general pattern has also been repeatedly observed in tropical bat assemblages (Gorresen and Willig 2004; Meyer and Kalko 2008; Struebig et al 2008; Klingbeil and Willig 2009; Arroyo-Rodríguez et al 2016; but see Cisneros et al 2015) and held true for our study. Regardless of landscape-scale, forest cover was the best predictor of species richness, having a strong positive effect, whereas the influence of configurational metrics varied in magnitude, but was consistently negative. These results mirror previous findings regarding the influence of landscape-scale forest cover in fragmented systems with an aquatic matrix (Meyer and Kalko 2008; Henry et al 2010), however, contrast with results from unflooded rainforest in Paraguay, Peru, Costa Rica and Mexico, where species richness was highest in partly deforested landscapes (Gorresen and Willig 2004; Klingbeil and Willig 2009; Cisneros et al 2015; Arroyo-Rodríguez et al 2016). These opposing results may reflect an interaction between regional species pools and landscape-specific environmental filters, especially the ones associated with the nature of the matrix habitats in which fragments are embedded. The matrix at the BDFFP is relatively homogeneous, being composed almost entirely of secondary forests (Laurance et al 2011). The higher compositional diversity of the humanized matrix habitats studied by Gorresen and Willig (2004), Klingbeil and Willig (2009), Cisneros et al (2015) and Arroyo-Rodríguez et al (2016) is probably associated with a greater variety of resources, which may consequently augment species diversity in moderately fragmented landscapes. These results highlight that the influence of matrix habitats on bat assemblages in forest fragments is highly context-specific (Meyer et al 2016), and are in line with previous findings that some agricultural habitats such as shade plantations can support a higher number of bat species than secondary forests (Faria 2006).

Edge density was positively correlated with total abundance and the abundances of both frugivores and gleaning animalivores at the smallest spatial scales, whereas the direction of the effect was negative at larger scales. This pattern matches recent findings from temperate areas, suggesting that at smaller scales edges may translate into increased foraging opportunities and promote connectivity between roosting and foraging areas, whereas at larger scales higher edge density implies increased habitat fragmentation and therefore negative effects on bat assemblages (Kalda et al 2015). Our modelling results regarding the response of gleaning animalivores to forest cover are also congruent with previous evidence that this ensemble is more sensitive to habitat modification than frugivores (Meyer et al 2016). However, contrary to our expectation, the associations of gleaning animalivores to configurational metrics were very similar to the ones observed for frugivorous bats. This indicates that the secondary regrowth habitats surrounding the BDFFP fragments may be buffering the impacts of forest fragmentation on these matrix-sensitive bats and suggests that fragment connectivity is of the utmost importance for the persistence of forest-associated species in modified landscapes.

Conclusions

The observed effects of fragment area on bat assemblages in the adjacent matrix highlights the importance of larger (> 10 ha) forest patches in the conservation of bat diversity, and in the regeneration and ecological recovery of anthropogenically disturbed forest habitats. Our results also emphasize that, although forest fragments and secondary forest habitats can be of conservation significance for tropical bats, old-growth forest is of irreplaceable value, adding to an increasing body of evidence that tropical biodiversity

is overwhelmingly dependent on the maintenance of vast tracts of primary habitat (Barlow et al 2007; Gibson et al 2011).

Fragmentation effects operate at multiple spatial scales and consequently the relative influence of local- and landscape-scale attributes on tropical biota can only be better understood through a multi-scale analysis as presented here. Considering multiple spatial scales can bridge apparently contradictory results of landscape features influencing assemblages differently at distinct spatial scales and therefore greatly benefit the successful delineation of landscape-level management actions aimed at abating the wave of habitat loss and fragmentation currently eroding the biodiversity of our planet's tropical regions.

Acknowledgments

We would like to thank the many volunteers and field assistants that helped during fieldwork, Tobias Jeppsson for providing a modified version of the hier.part function for the hierarchical partitioning analysis, and the BDFFP management team for logistic support. Funding was provided by a Portuguese Foundation for Science and Technology (FCT) project grant (PTDC/BIA-BIC/111184/2009). R.R. was supported by FCT (SFRH/BD/80488/2011), A.L.-B. by (FCT PD/BD/52597/2014) and CNPq (160049/2013-0), P.E.D.B. by CAPES and M.C. by Academy of Finland (grant #257686). Research was conducted under ICMBio permit (26877-2) and is publication 698 in the BDFFP technical series.

Online Supplementary Material can be found at:

http://www.r-rocha.com/wp-content/uploads/2015/09/Supplementary-Material-PhD-thesis-Ricardo-Rocha-Chapter-2.pdf

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Supplementary Material

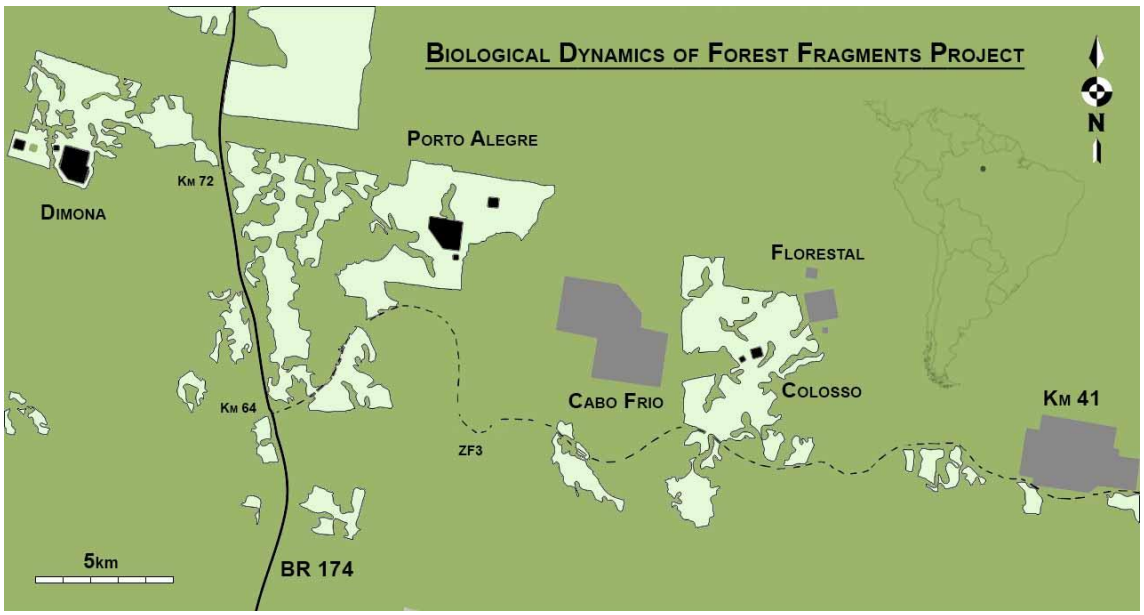

Fig. S1 Map of the study area at the BDFFP, Central Amazon, Brazil. Black areas denote the forest fragments in Dimona, Porto Alegre, and Colosso camps and dark grey stands for the continuous forest reserves in Cabo Frio, Florestal and Km 41 camps. Light green areas represent the secondary forest matrix and dark green the continuous forest.

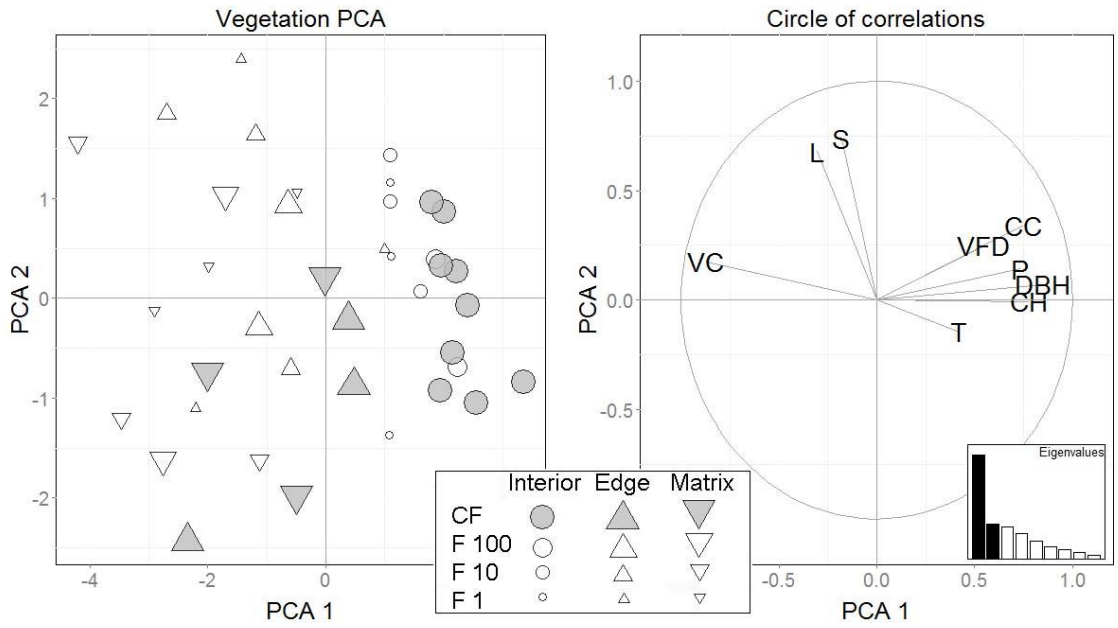

Fig. S2 Principal components analysis examining the covariation between vegetation structure variables. CC = canopy cover, CH = canopy height (m), DBH = average of the DBH measures of trees ≥ 10 cm, L = number of lianas, P = number of palms, S = number of woody stems (DBH < 10 cm), T = number of trees (DBH > 10), VC = number of *Vismia* and *Cecropia* trees, VFD = vertical foliage density.

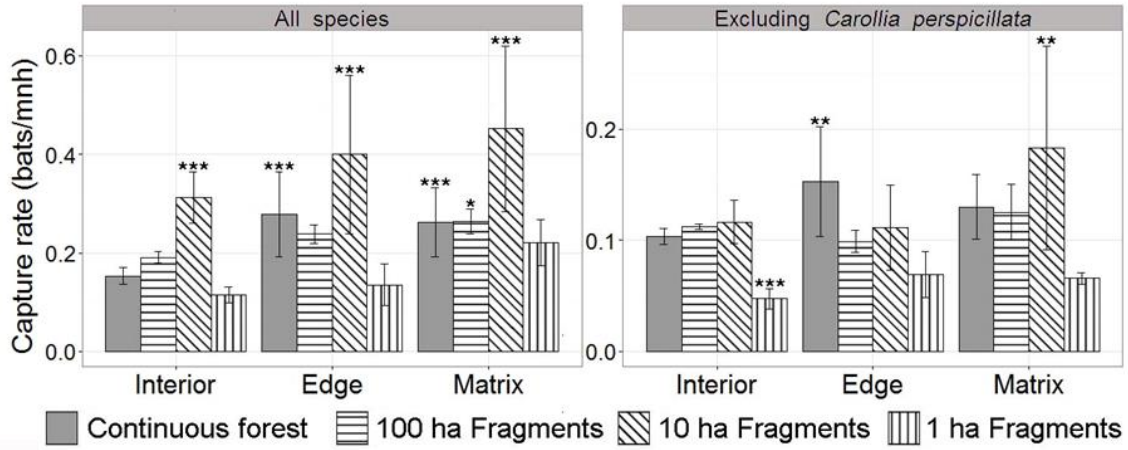

Fig. S3 Mean (± SE) capture rate (bats/mnh) across the interior-edge-matrix as well as fragment-size gradient, considering all species and excluding the most common one (*Carollia perspicillata*). Asterisks denote significant differences relative to CF interiors (*** P < 0.001; ** P < 0.01; * P < 0.05).

Table S1 Bat species sampled in the BDFFP, Central Amazon, Brazil. Ensemble abbreviations: AEIN = aerial insectivore; FRUG (C) = canopy frugivore; FRUG (S) = shrub frugivore; GLAN = gleaning animalivore; SANG = sanguivore.

		Continuous Forest			Fragments			
Taxon	**Ensemble**	**Interior**	**Edge**	**Matrix**	**Interior**	**Edge**	**Matrix**	**Total**
Emballonuridae								
Centronycteris maximiliani	AEIN					1		1
Cormura brevirostris	AEIN	2	2		3			7
Saccopteryx bilineata	AEIN					1	2	3
Saccopteryx leptura	AEIN	1			3	1	1	6
Furipteridae								
Furipterus horrens	AEIN	1						1
Phyllostomidae								
Ametrida centurio	FRUG (C)		2	1		2	2	7
Anoura caudifer	NECT	1	1		1	1	1	5
Artibeus cinereus	FRUG (C)	13	3	2	7	4	7	36
Artibeus concolor	FRUG (C)	4	11	9	8	9	28	69
Artibeus gnomus	FRUG (C)	10	6	2	6	5	10	39
Artibeus lituratus	FRUG (C)	24	3	8	5	1	15	56
Artibeus obscurus	FRUG (C)	23	4	5	25	31	46	134
Artibeus planirostris	FRUG (C)	10	1		8		3	22
Carollia brevicauda	FRUG (S)	18	23	19	29	16	28	133
Carollia castanea	FRUG (S)				3			3
Carollia perspicillata	FRUG (S)	300	127	134	637	427	513	2138

Choeroniscus minor	NECT	1			6			7
Chrotopterus auritus	GLAN	3			2			5
Desmodus rotundus	SANG	7	1		2		1	11
Glossophaga soricina	NECT	2			5	1		8
Glyphonycteris daviesi	GLAN	3					2	5
Glyphonycteris sylvestris	GLAN	1						1
Lampronycteris brachyotis	GLAN				1			1
Lonchophylla thomasi	NECT	13	1	1	16	3	1	35
Lophostoma brasiliense	GLAN	1				4		5
Lophostoma carrikeri	GLAN	1			1	2	1	5
Lophostoma schulzi	GLAN	4		1	2	1	1	9
Lophostoma silvicolum	GLAN	52	4	1	14	10	9	90
Mesophylla macconnelli	FRUG (C)	16			5	2	1	24
Micronycteris hirsuta	GLAN				1		1	2
Micronycteris megalotis	GLAN	1	1	1	1			4
Micronycteris microtis	GLAN	5	1	3	3	1	2	15
Micronycteris schmidtorum	GLAN				1			1
Mimon crenulatum	GLAN	26	15	14	16	12	9	92
Phylloderma stenops	GLAN	7	1	1	3	2	2	16
Phyllostomus discolor	NECT	3	3		3		1	10
Phyllostomus elongatus	GLAN	21	2		7	2	1	33
Phyllostomus hastatus	GLAN	1			1	1		3
Platyrrhinus helleri	FRUG (C)					2	1	3
Rhinophylla pumilio	FRUG (S)	117	41	34	180	83	89	544
Sturnira tildae	FRUG (S)	1	1	5	1	4	14	26

Tonatia saurophila	GLAN	32	2	2	25	4	2	67
Trachops cirrhosus	GLAN	71	6	5	30	2	11	125
Trinycteris nicefori	GLAN	4		1	2	2	1	10
Uroderma bilobatum	FRUG (C)				1	2	2	5
Vampyressa pusilla	FRUG (C)		1					1
Vampyriscus bidens	FRUG (C)	10		3	5	1		19
Vampyriscus brocki	FRUG (C)				2	1		3
Mormoopidae								
Pteronotus parnellii	AEIN	118	22	14	53	25	40	272
Vespertilionidae								
Eptesicus brasiliensis	AEIN	1	1			1		3
Myotis nigricans	AEIN	1	1		1			3
Myotis riparius	AEIN	16	18	3	26	13	10	86
Rhogeessa io	AEIN						1	1
Total captures		**946**	**305**	**269**	**1151**	**680**	**859**	**4210**

Table S2 Summary of vegetation structure variables. CC = percent canopy cover, CH = canopy height (m), DBH = average (cm) of the DBH measures of trees ≥ 10 cm, L = number of lianas, P = number of palms, S = number of woody stems (DBH < 10 cm), T = number of trees (DBH ≥ 10 cm), VC = number of *Vismia* and *Cecropia* trees, VFD = vertical foliage density (values for CH, DBH, L, T, VC and VFD are also presented in Farneda et al 2015, Table S2). Results are presented as mean ± 1SD.

Habitat category	CC	CH	DBH	L	P	S	T	VC	VFD
Continuous forest interior	85.4 ± 5.2	12.4 ± 3.2	24.8 ± 1.3	1.2 ± 0.4	14.4 ± 5.1	101.1 ± 27.8	10.9 ± 2.7	0.2 ± 0.4	519.4 ± 112.8
Continuous forest edge	78.6 ± 5.3	7.8 ± 1.8	17.7 ± 1.5	1.7 ± 1.2	5.7 ± 3.2	70.3 ± 10.7	11.3 ± 2.1	1.7 ± 0.6	455.3 ± 134.3
Continuous forest matrix	79.1 ± 0.3	8.6 ± 2.8	16.3 ± 1.5	1.7 ± 0.6	4.7 ± 2.1	83.7 ± 43	9.3 ± 1.2	2.3 ± 1.5	460.3 ± 164.1
100 ha fragment interior	83.6 ± 0.9	11.3 ± 1.6	23 ± 1.4	1	10.5 ± 6.4	92 ± 29.7	8	0	722.5 ± 98.3
100 ha fragment edge	74.2 ± 5.5	8.7 ± 0.6	17.5 ± 0.7	2.5 ± 0.7	4.5 ± 2.1	109.5 ± 13.4	11 ± 1.4	3	575 ± 89.1
100 ha fragment matrix	71.6 ± 2	7.1 ± 0.5	17 ± 1.4	2.5 ± 2.1	2 ± 2.8	105 ± 28.3	7.5 ± 0.7	2	463 ± 1.4
10 ha fragment interior	87.4 ± 1	9.7 ± 1.2	23 ± 3	2.3 ± 1.2	7 ± 1	96 ± 15.6	7.7 ± 0.6	0.7 ± 0.6	639 ± 53.7
10 ha fragment edge	79.6 ± 2.5	6.7 ± 0.6	20.7 ± 6.4	3 ± 1	4.7 ± 2.1	123.3 ± 54.2	8.7 ± 1.5	9.3 ± 10.2	438 ± 67.9
10 ha fragment matrix	76.5 ± 1.3	6.6 ± 1.5	14.3 ± 1.5	1.7 ± 2.1	2.7 ± 2.1	117.7 ± 32.1	8.3 ± 4.9	12.3 ± 9.3	362.7 ± 29.5
1 ha fragment interior	84.6 ± 2	7.6 ± 0.7	23.3 ± 3.8	2 ± 1	11 ± 5	88 ± 42.5	7.7 ± 0.6	0	547.7 ± 89.4
1 ha fragment edge	79.1 ± 10.2	7.1 ± 0.8	18 ± 3.6	2.3 ± 1.5	5 ± 4	130 ± 34.7	10 ± 2.6	2.3 ± 2.1	519 ± 24
1 ha fragment matrix	75.1 ± 6.7	7.3 ± 1.7	18.3 ± 2.3	3.3 ± 0.6	5 ± 3.6	95.3 ± 25.8	7.3 ± 2.3	4.3 ± 3.2	468.3 ± 137

Table S3 Variable loadings, eigenvalues and proportion of variance explained by the first two axes of the principal components analysis examining the covariation between vegetation structure variables.

Vegetation structure variables	**PCA 1**	**PCA 2**
Canopy cover	0.39	0.30
Number of woody stems (DBH <10 cm)	-0.09	0.66
Number of trees (DBH >10)	0.22	-0.13
Number of palms	0.38	0.13
Number of lianas	-0.16	0.61
Number of *Vismia* spp. and *Cecropia* spp. trees	-0.45	0.16
Average of the DBH measures of trees ≥10 cm	0.44	0.06
Canopy height (m)	0.40	-0.01
Vertical foliage density	0.28	0.22
Eigenvalue	3.80	1.30
% explained	42.02	14.20
Cumulative proportion	42.02	56.04

Table S6 – Capture rate (bats/mnh) of all frugivores, shrub frugivores, canopy frugivores, gleaning animalivores, aerial insectivores (*Pteronotus parnellii*) and nectarivores for interior, edge and matrix sites of the different habitat categories (continuous forest and 1 ha, 10 ha and 100 ha fragments) across the BDFFP landscape. Values represent mean ± SE.

Habitat	Frugivores	Shrub frugivores	Canopy frugivores	Gleaning animalivores	Aerial insectivores	Nectarivores
Continuous forest interior	0.088 ± 0.013	0.072 ± 0.002	0.016 ± 0.012	0.041 ± 0.004	0.020 ± 0.004	0.003 ± 0.001
Continuous forest edge	0.219 ± 0.08	0.189 ± 0.019	0.030 ± 0.063	0.031 ± 0.006	0.022 ± 0.001	0.005 ± 0.002
Continuous forest matrix	0.219 ± 0.071	0.189 ± 0.019	0.030 ± 0.051	0.029 ± 0.010	0.014 ± 0.002	0.001 ± 0.001
100 ha fragment interior	0.135 ± 0.008	0.118 ± 0.006	0.017 ± 0.002	0.028 ± 0.007	0.022 ± 0.001	0.005 ± 0.002
100 ha fragment edge	0.200 ± 0.008	0.192 ± 0.004	0.007 ± 0.003	0.022 ± 0.016	0.013 ± 0.007	0.003 ± 0.003
100 ha fragment matrix	0.236 ± 0.015	0.184 ± 0.001	0.052 ± 0.013	0.007 ± 0.007	0.016 ± 0.001	0.003 ± 0.003
10 ha fragment interior	0.265 ± 0.045	0.252 ± 0.002	0.013 ± 0.043	0.032 ± 0.008	0.005	0.010 ± 0.002
10 ha fragment edge	0.374 ± 0.158	0.328 ± 0.033	0.046 ± 0.124	0.020 ± 0.002	0.005 ± 0.001	0.001 ± 0.001
10 ha fragment matrix	0.399 ± 0.162	0.333 ± 0.052	0.066 ± 0.011	0.030 ± 0.010	0.021 ± 0.005	0.001 ± 0.001
1 ha fragment interior	0.100 ± 0.016	0.091 ± 0.003	0.009 ± 0.014	0.006 ± 0.004	0.007 ± 0.004	0.002 ± 0.002
1 ha fragment edge	0.110 ± 0.034	0.095 ± 0.007	0.015 ± 0.029	0.012 ± 0.006	0.011 ± 0.010	0.002 ± 0.001
1 ha fragment matrix	0.205 ± 0.043	0.193 ± 0.005	0.012 ± 0.042	0.008 ±0.004	0.008 ± 0.003	0

CHAPTER 3

Does sex matter? Gender-specific responses to forest fragmentation in Neotropical bats

Rocha, R., Ferreira, D., López-Baucells, A., Farneda, F.Z., Carreiras, J.M.B, Palmeirim, J.M. & Meyer, C.F.J. Does sex matter? Gender-specific responses to forest fragmentation in Neotropical bats. *in press*

CHAPTER 3

Does sex matter? Gender-specific responses to forest fragmentation in Neotropical bats

ABSTRACT

Understanding the consequences of habitat modification on wildlife communities is central to the development of conservation strategies. However, albeit male and female individuals of numerous species are known to exhibit differences in habitat use, sex-specific responses to habitat modification remain little explored. Here, we used a landscape-scale fragmentation experiment to assess, separately for males and females, the effects of fragmentation on the abundance of eight Neotropical bats. We predicted that sex-specific responses would arise from higher energetic requirements from pregnancy and lactation in females. Analyses were conducted independently for each season and, for two of the most common species (*Carollia perspicillata* and *Rhinophylla pumilio*), we further investigated the joint responses to local and landscape-scale metrics of habitat quality, composition and configuration. Although males and females responded similarly to a fragmentation gradient composed by continuous forest, fragment interiors, edges and matrix habitats, for three species we found marked differences between sexes in habitat use for at least one of the seasons. Whereas the sex ratio varied little in continuous forest and fragment interiors, females were found to be more abundant than males in edge and matrix habitats; for most species, this difference was more prominent in the dry season. Responses to local- and landscape-scale abundance predictors differed between sexes for *C. perspicillata* and *R. pumilio*, with differences being more pronounced in the dry season. The results suggest considerable sex-mediated responses to

forest disruption and degradation in tropical bats and complement our understanding of the impacts of fragmentation on tropical forest vertebrate communities.

Key words: Intraspecific variation, Sex differences; Seasonality; Secondary forest; Spatial scale; Vegetation structure.

INTRODUCTION

A rapidly growing human population and increasing *per capita* consumption are leading to widespread conversion and degradation of natural habitats, further exacerbating the already precarious status of the planet's ecosystems (Newbold *et al.* 2016). Habitat fragmentation and degradation rank among the most serious threats responsible for the current biodiversity crisis (Haddad *et al.* 2015; Barlow *et al.* 2016) and their impacts are of particular concern in the mega-diverse tropical forests, home to most of the planet's terrestrial species (Malhi *et al.* 2014).

Understanding species patterns of habitat use and how local habitat quality, as well as landscape composition and configuration interact to shape communities in fragmented landscapes is paramount to framing effective conservation strategies (Villard & Metzger 2014). However, within the thriving fragmentation literature, intraspecific differences in species responses to local and landscape-scale characteristics have received little attention. Among those, sex-specific responses have been particularly neglected, despite their

overwhelming importance for the dynamics and long-term persistence of natural communities (Frank *et al.* 2016).

Accounting for differences between sexes in the evaluation of animal responses to anthropogenic pressures is important as males and females may differ, sometimes greatly, in key features of their biology such as parental care (e.g. Lucass *et al.* 2016), anti-predator-behaviour (e.g. Curlis *et al.* 2016), habitat selection (e.g. Penado *et al.* 2015) and physiological responses to stress levels (e.g. Small & Schoech 2014). These dissimilarities can translate into differential susceptibility to fragmentation between sexes and consequently result in locally-skewed sex ratios, potentially leading to greater extinction risks (Le Galliard *et al.* 2005, Melbourne & Hastings 2008).

Sexual dimorphism is rare among bats, the second most diverse mammalian order (Altringham 2011). However, gender-specific differences in attributes such as aggressiveness towards conspecifics (Ancillotto & Russo 2014), prey composition (Mata *et al.* 2016) and selection of roosting and foraging areas (Encarnação 2012, Angell *et al.* 2013, Istvanko *et al.* 2016, Down *et al.* 2016) have been reported for numerous species of mostly temperate bats. Yet, notwithstanding some notable exceptions (e.g. Evelyn & Stiles 2003, Henry & Kalko 2007, Henry *et al.* 2007, Frank *et al.* 2016), differences between sexes in their tropical counterparts still remain largely unexplored. However, these differences should be commonplace as tropical bats also have to balance their sex-specific energy requirements with the spatiotemporal variability of resources and the compositional and configurational heterogeneity of the landscape (Cisneros *et al.* 2015a).

The reproductive phenology of many tropical bats is strongly correlated with environmental conditions and resource availability (Ramos Pereira *et al.* 2010, Durant *et al.* 2013). Still, despite timing their life-cycle to match periods of peak food availability, female bats may be constrained by the elevated energetic requirements associated with pregnancy and lactation, which might force them to alter their foraging time budgets and limit their habitat use to the most resource-rich areas (Lintott *et al.* 2014). Although habitat quality might not be as critical to males and non-breeding females, the former might be affected by higher intra-specific competition, leading to the displacement of poorly competitive same-sex juveniles from resource-rich habitats (Henry *et al.* 2007).

Tropical bats, like numerous other taxa, are affected by fragmentation and habitat degradation (Meyer *et al.* 2016). Their responses have been found to be scale-sensitive, highly species- and ensemble-specific and to vary according to seasonal variation in resource abundance (Arroyo-Rodríguez *et al.* 2016. Cisneros *et al.* 2015a, Chambers *et al.* 2016, Rocha *et al.* 2017, Ferreira *et al.* 2017). Matrix type and condition impose influential filters on their local assemblages (Farneda *et al.* 2015, Mendenhall *et al.* 2014) and local-scale vegetation structure, by constraining flight and access to food resources, influences species' occurrence and abundance (Marciente *et al.* 2015). However, no study has yet investigated how male and female bats differ in their responses to local and landscape-scale characteristics in fragmented landscapes.

Here, we investigated how the abundance of male and female Amazonian bats differed along a disturbance gradient composed of continuous primary forest, fragment interiors, forest edges and secondary forest matrix habitats. Additionally, for the two most common species (*Carollia perspicillata* and *Rhinophylla pumilio*), we examined how male and female

abundance is influenced by vegetation structure (local-scale variable) and, for five spatial scales, by metrics of landscape composition and configuration. Due to the expectation that sex-specific differences in habitat use reflect seasonal variation in resource availability we conducted separate analyses for the wet and dry seasons. We hypothesized that the sex ratio would change across the disturbance gradient due to the increased energetic demands of females associated with pregnancy and lactation and we predicted that the capture rate of frugivorous female bats during the peak reproductive periods would be particularly high in secondary forest due to increased fruit availability. Additionally, we anticipated that since reproduction imposes high fluctuations in energetic demands, female-male consistency in the responses of *C. perspicillata* and *R. pumilio* to local and landscape-scale characteristics would vary between dry and wet seasons. Specifically, since the peak pregnancy period of both species in our study area occurs in the dry season (Bernard 2002), we predicted that females, due to higher energetic demands associated with pregnancy, would respond more strongly to compositional metrics (and hence fruit availability) in the dry season, whereas males would present similar responses to local and landscape-scale attributes in both the dry and wet seasons.

METHODS

Study area

Fieldwork took place at the Biological Dynamics of Forest Fragments Project (BDFFP), a whole-ecosystem fragmentation experiment located ~80 km north of Manaus (2°25'S, 59°50'W), Brazilian Amazon (Fig. 1) (Laurance *et al.* 2011). The landscape is characterized by a mosaic of continuous *terra firme* forest and primary forest fragments surrounded by a matrix of secondary forest. Primary forest canopy is 30–37 m tall, with emergent trees up to 55 m (Laurance *et al.* 2011). Annual rainfall in the region ranges from 1,900 to 3,500 mm, with a wet season from November to June (precipitation can exceed 300/month) and a dry season from July to November (precipitation below 100/month) (INPA 2014). Flowering is concentrated in the transition between dry and wet seasons and fruiting peaks at the onset of the wet season (Haugaasen & Peres 2005, Bentos *et al.* 2014). Eleven experimental primary forest fragments categorized into size classes of 1, 10 and 100 ha were isolated in the early-80s by clearing and, in some cases, also burning the surrounding forest. Fragment distance from continuous forest ranges from 80 to 650 m and each was re-isolated on 3-4 occasions prior to this study, most recently between 1999 and 2001 (Laurance *et al.* 2011). The matrix is composed by secondary forests in different successional stages (Carreiras *et al.* 2014) and is dominated mainly by *Vismia* spp. (areas that were cleared and burned) and *Cecropia* spp. (areas cleared without fire) (Mesquita *et al.* 2015).

Bat sampling

Sampling was conducted in eight forest fragments (three of 1 ha, three of 10 ha and two of 100 ha; Dimona, Porto Alegre and Colosso camps) and nine control sites in three areas of continuous forest (Cabo Frio, Florestal and Km 41 camps) (Fig. 1). Bat mist netting took place in the interiors and at the edges of all eight fragments, as well as at eight sites in the adjacent secondary forest matrix, 100 m from the edge of each fragment. A similar sampling scheme was adopted in continuous forest, whereby nine sites were sampled in the interior, three at the edge, and three in the secondary forest matrix, 100 m from the forest edge. Accordingly, a total of 39 sites were sampled. Distances between interior and edge sites of continuous forest and fragments were respectively 1118 ± 488 and 245 ± 208 m (mean ± SD).

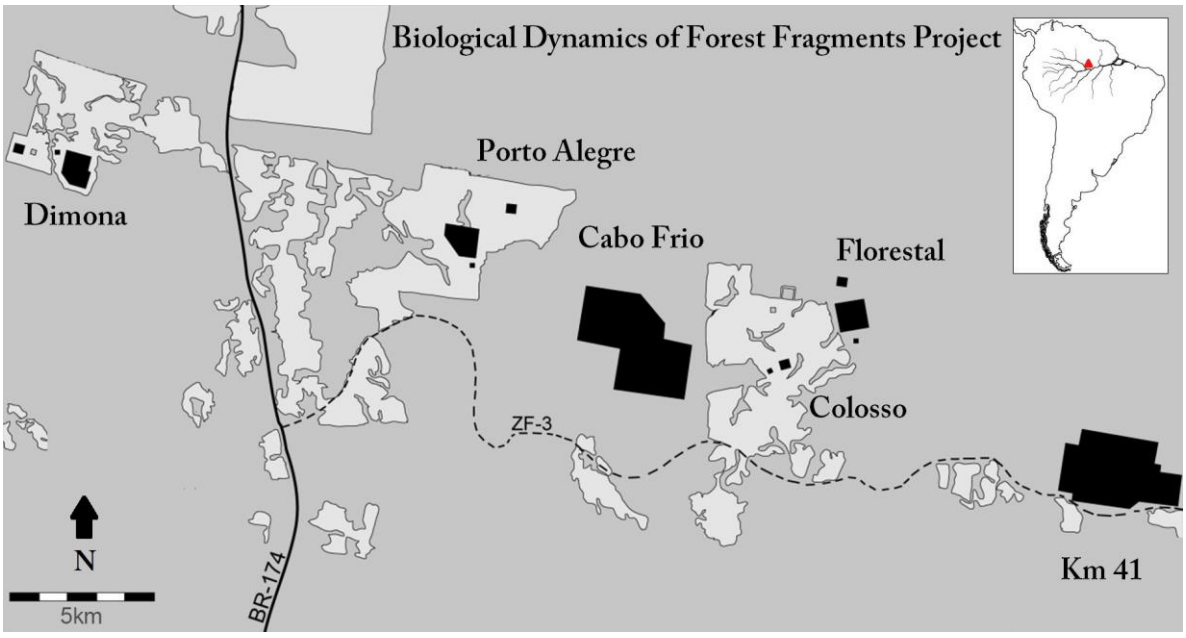

FIGURE 1. Map of the study area at the BDFFP, Central Amazon, Brazil. Black areas denote the forest fragments in Dimona, Porto Alegre, and Colosso camps as well as continuous forest sites in Cabo Frio, Florestal and Km 41 camps. Light grey areas represent the secondary

forest matrix and dark grey the continuous forest. The triangle on the map of South America denotes the location of the study area.

Bats were sampled during the dry (July to November of 2011 and 2012; two visits each year) and wet seasons (February to June of 2012 and 2013; two visits each year) using 14 ground-level mist nets (12 x 3 m, 16 mm mesh, ECOTONE, Poland) in continuous forest and fragment interiors and seven at edge and matrix sites. Sampling started at dusk and nets were left open for six hours, being revised every ~20 minutes. Capture effort was 10726 mist-net hour (mnh) in the wet season and 7924 mnh in the dry season (1 mnh equals one 12-m net open for 1h). Bias in capture rates due to net shyness was avoided by spacing same-site surveys 3 to 4 weeks apart (Marques *et al.* 2013). Species identification followed Lim & Engstrom (2001) and Gardner (2007) and taxonomy follows the latter. All non-phyllostomid species other than *Pteronotus parnellii* are poorly sampled with mist nets (Kalko 1998) and were therefore excluded from the analyses.

Female-male abundance across the interior-edge-matrix gradient

Differences in abundance between sexes, seasons (dry and wet) and habitat types (interior, edge and matrix) were assessed using general linear mixed-effects models (GLMMs). For each species, the number of captured individuals was used as response variable (Poisson distribution, log-link function) and sex, season and habitat type were specified as fixed, interacting effects. Due to the high model complexity when implementing a three-way interaction, we decided to instead use two-way interactions between sex and habitat type for each season separately. Reflecting our nested sampling design and to account for potential

autocorrelation between sites within the same location, models included a random term nesting "site" within "location" (the latter referring to the six research camps at the BDFFP; Fig 1). Each site's total capture effort (log number of mnh) was incorporated as a model offset. Significant effects were evaluated for each species via likelihood-ratio tests and multiple comparison tests with Tukey contrasts (adjusted *P* values reported) in the R package "*multcomp*" (Hothorn *et al.* 2008). Analyses were restricted to the eight species that had more than 30 captures for each sex and had at least 10 captures per season.

Female-male responses to local and landscape scale-variables

Vegetation structure

Vegetation structure was quantified within three 100 m^2 (5 x 20 m) plots established 5 m from each side of the mist net transects. In each plot the following variables were quantified: i) diameter at breast height (DBH), ii) percent canopy cover, iii) number of woody stems (DBH < 10 cm), iv) number of trees (DBH ≥ 10 cm), v) number of palms, vi) number of lianas, vii) number of pioneer trees (genera *Vismia* and *Cecropia*), viii) tree height and, ix) vertical foliage density. Vegetation variables were then submitted to a Principal Components Analysis (PCA) and the score values for the first axis (PCA1 – explaining 42% of the total variance and representing a gradient from simpler vegetation structure, typical of secondary forests [negative values] to more complex vegetation structure, typical of primary forest [positive values]) were subsequently used as predictor variable for local vegetation structure (LVS). Details regarding the quantification of the vegetation variables and PCA analysis are given in the previous chapter and in Rocha *et al.* (2017).

Landscape composition and configuration

Landscape metrics were obtained from a land cover map of the BDFFP landscape from 2011. The map was based on the analysis of a quasi-annual time series of Landsat Thematic Mapper data (30 m resolution) from the 1970s up to 2011 (Carreiras *et al.* 2014). For this study, the map was classified into four land cover types, representing: i) continuous primary forest (PF); ii) early-stage secondary forest (SF) (≤ 5 years); iii) intermediate-stage SF (6-15 years); iv) advanced-stage SF (≥ 16 years) (see Carreiras *et al.* 2014 for classification details) (Fig. S1). Selection of metrics of landscape composition and configuration was based on previous analyses of bat-environment relationships (Meyer & Kalko 2008, Klingbeil & Willig 2009, Klingbeil & Willig 2010, Avila-Cabadilla *et al.* 2012, Cisneros *et al.* 2015b, Arroyo-Rodríguez *et al.* 2016, Rocha *et al.* 2017) and metrics were computed for landscape buffers with radii of 250, 500, 750, 1000 and 1500 m surrounding each of the 39 sampling sites. These buffer sizes were chosen as they encompass the home ranges of different-sized bat species and at the same time minimize buffer overlap (Meyer & Kalko 2008). Apart from mean nearest neighbour distance (calculated using the software QGIS), the following metrics were calculated using the R package "SDMtools" (VanDerWal *et al.* 2011) to represent: (a) landscape composition (primary forest cover [PFC], secondary forest cover – initial stage [SFC1], intermediate stage [SFC2] and advanced stage [SFC3]) and (b) landscape configuration (edge density [ED], patch density [PD], mean nearest neighbour distance [MNND] and mean shape index [MSI]). Following McGarigal (2014), the MNND was calculated as the mean of the shortest straight-line distance between the sampling site and each of its nearest neighbours of the same class. When a given buffer contained only one

patch of PF we calculated MNND as the distance between that patch and the nearest one in the next larger buffer.

Relative importance of local and landscape predictors

Independently for each sex and season, we examined the relative importance of LVS and landscape-scale metrics in affecting species abundance at the five focal spatial scales using Poisson GLMMs. The number of captures at each site was used as response variable and, as above, "site" nested within "location" was included as a random term and log(effort) was included as an offset. Multicollinearity between predictor variables was investigated by calculating i) variance inflation factors (VIF) and ii) pairwise Pearson correlations. "Severe" collinearity is present when VIFs > 10 (Neter *et al.* 1996), therefore, following Benchimol & Peres (2015), we considered variables with VIF ≤ 6 suitable to be included in the analyses. However, we found that variables with VIF < 6 differed between spatial scales and the same was found for correlation values with a Pearson's $r > 0.6$. We therefore dismissed these analyses as the selection of distinct predictors for different buffer sizes would preclude meaningful comparisons between scales. As such, we opted to include all the predictor variables in our GLMMs. Although this can lead to some multicollinearity and consequently jeopardize statistical inference (Dormann *et al.* 2013), we consider that each predictor represents a particular avenue of interaction between ecological mechanisms and bat abundances and, consequently, omission of predictor variables at a given spatial scale could undermine the estimates of the relative importance for the remaining predictors (Smith *et al.* 2009). These analyses were limited to the two most common species (*C. perspicillata* and *R.*

pumilio) as low number of captures for either sex or season precluded separate analyses for other species.

For each species, sex and spatial scale, separate sets of candidate models were chosen a priori, comprising plausible combinations of local (LVS) and landscape predictors (PFC, SFC1, SFC2, SFC2, SFC3, ED, PD, MNND and MSI). The following models were considered (i) all predictors, (ii) each predictor individually, (iii) LVS and landscape composition predictors, (iv) LVS and landscape configuration predictors, (v) composition and configuration predictors (vi) composition predictors only, (vii) configuration predictors only (viii) SFC predictors only, (viii) LVS and SFC predictors, (ix) all predictors without SFC predictors and (x) all predictors without PFC predictor. GLMMs were fitted in the "*lme4*" package in R (Bates 2010) and selection of the best-fit models was performed through Akaike's Information Criterion corrected for small sample sizes (AICc). Model averaging, conducted in the "*AICcmodavg*" package (Mazerolle 2016), was used to obtain parameter estimates for the predictors when multiple models had a $\Delta AICc \leq 2$ (Burnham & Anderson 2002). Moran's *I* tests were used to assess potential spatial autocorrelation of the residuals of our best-fit GLMMs. For these best-fit models, the relative importance of each predictor was determined through hierarchical partitioning analysis using the "*hier.part*" package (Walsh *et al.* 2013), modified to include "log(effort)" as a model offset (Jeppsson *et al.* 2010). Following Benchimol & Peres (2015) and Rocha *et al.* (2017), hierarchical partitioning analysis was conducted considering only the fixed effects.

For each species and independently for each season, the consistency between predictor variables included in the best models for each sex was calculated via a model consistency index (Gutzwiller & Barrow Jr 2001). This was computed as the number of common

predictors with the same direction of effect for each sex in each season, divided by the total number of predictors included in the best-fit models. High between-sex variation in species-environment relations stands for low model consistency and vice-versa. All analyses were conducted in R v3.1.3 software (R Development Core Team 2013).

RESULTS

We captured a total of 3431 adult bats representing 44 species (43 phlyllostomids and one mormoopid, *P. parnellii*). Females comprised nearly two thirds (2097, 61.1%) of all captures (Table S1). The female-male capture ratio averaged 1.42 (± 0.1, SD) across the different habitat categories for the wet season and 1.83 (± 0.08) for the dry season.

Sex differences in capture rates across the interior-edge-matrix gradient

Of the eight species analysed, seven and five exhibited significant effects for the interaction between sex and habitat type for the dry and wet seasons, respectively (Table S2). However, for only three of these species (*C. perspicillata*, *P. parnellii* and *R. pumilio*) the differences in the abundance of female and male bats were significant based on multiple pairwise comparisons (Fig. 2; Tables S3 in Online Supplementary Material). While for most species female-male numbers varied little in continuous forest, and to a lesser extent in fragment interiors, in edge and matrix habitats females tended to outnumber males in both seasons, with the difference being more pronounced in the dry than in the wet season.

For *C. perspicillata*, significant differences between the number of captured females and males were restricted to the dry season, during which the capture rate of females was always

higher than the capture rate of males in all considered habitats (Fig. 2). On the other hand, for *R. pumilio*, females outnumbered males in the matrix during the wet season and at both fragment edges and in the matrix in the dry season. For *P. parnellii*, females had higher capture rates than males in continuous forest and fragments during the wet season and at edges during the wet and dry seasons (Fig. 2).

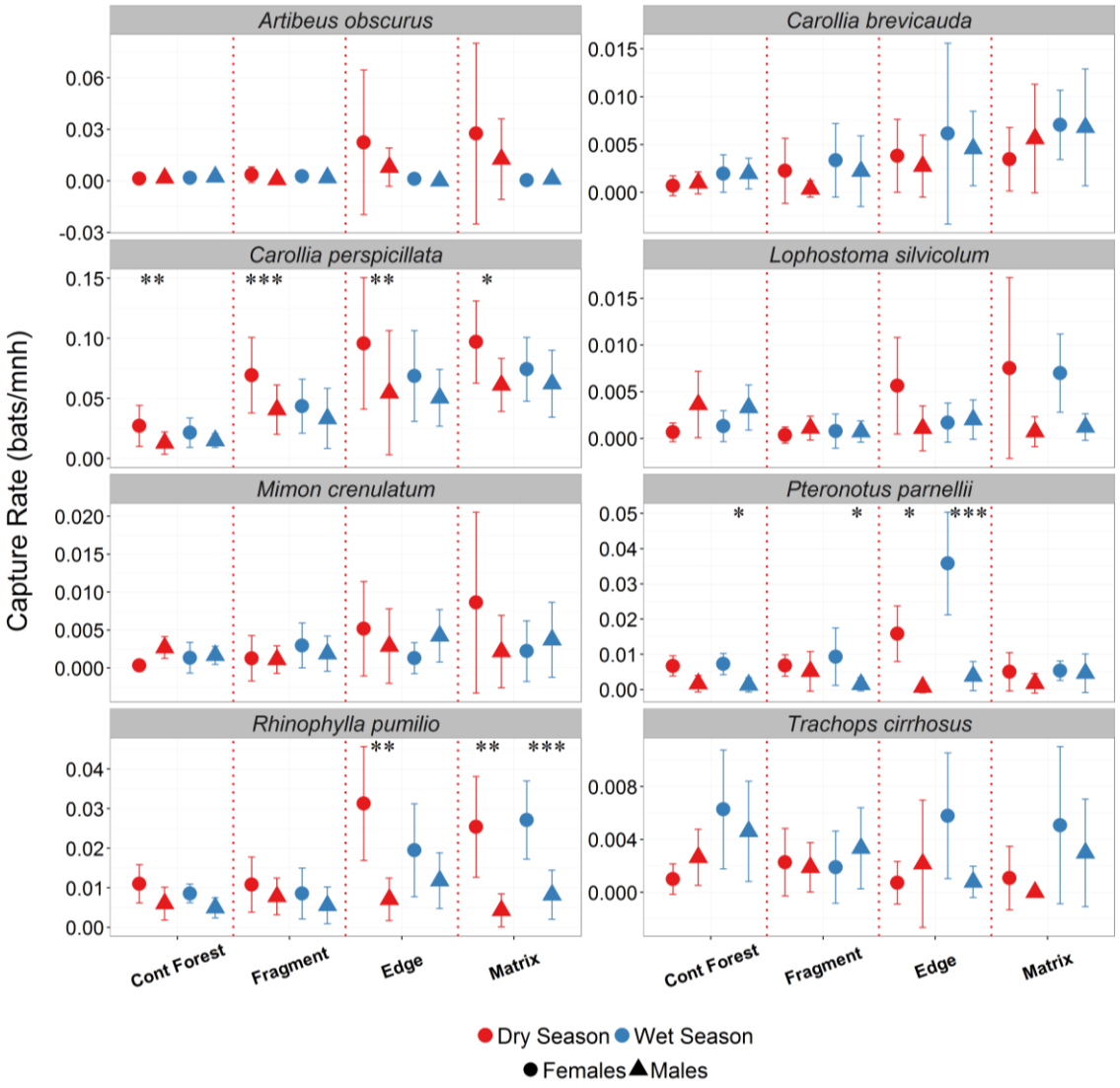

FIGURE 2. Variation in mean (± CI) capture rate (bats/mnh) of males and females across different habitat types in the BDFFP landscape in the dry and wet seasons. Significant differences in capture rates between sexes are indicated as *** $P < 0.001$, ** $P < 0.01$ and * $P < 0.05$.

Sex differences in responses to local and landscape scale-variables

The relative importance of vegetation structure and compositional and configurational landscape characteristics differed between sexes for both *C. perspicillata* and *R. pumilio* (Fig. 3 and 4; See Tables S4 and S5 in Online Supplementary Material). None of the GLMMs yielded spatially autocorrelated residuals (Table S6 in Online Supplementary Material) and for both species model consistency was higher in the wet season (71.4% *C. perspicillata*; 16.7% *R. pumilio*) than in the dry season (22.2% *C. perspicillata*; 0% *R. pumilio*).

For *C. perspicillata*, the abundance of females in the dry season was nearly exclusively dictated by the amount of PFC, to which the response was negative across all scales. Configurational metrics had no influence at the smallest scales (250 and 500 m) and only PD was shown to negatively affect abundance at the largest scales (≥ 750 m). For males during the dry season the influence of vegetation structure and configurational metrics was almost negligible. They were less influenced by PFC, but instead responded more strongly to the amount of secondary forest cover, especially, at larger spatial scales (≥ 750 m) to SFC3. During the wet season, females showed a negative response towards LVS across all scales and to PFC, PD and MSI at intermediate scales (500, 750 and 1000 m). For these scales however, the responses to ED were positive. During this season, male responses nearly mirrored those of females (Fig 3).

For *R. pumilio*, female abundance during the dry season was nearly exclusively related to LVS across all scales (negative association). By contrast, male responses were all neutral apart from ED at the smallest scale, for which the response was positive. During the wet season LVS was again the metric with more relevance for females, negatively influencing

abundance across all scales. For males, LVS had also a negative influence, but its relevance slightly decreased with increasing scale. The opposite was true, albeit the direction of the effect was positive, for SFC3 for which there was an increase in predictor relevance from smaller to larger scales.

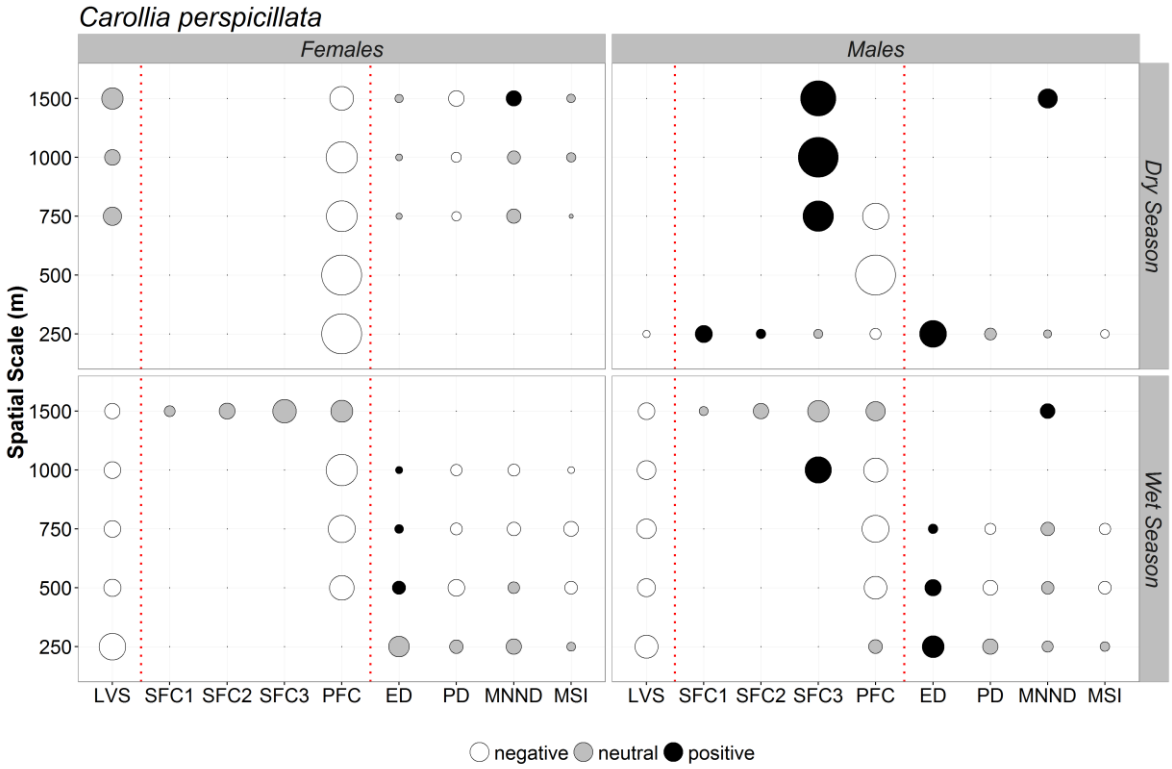

FIGURE 3. Summary results of model averaging of the best-fit generalized linear mixed models (Akaike differences < 2 from the best model) exploring the association between local and landscape-scale predictors and the abundance of male and female *Carollia perspicillata* at five focal scales across the Biological Dynamics of Forest Fragments Project. Symbol size is proportional to the variation explained by the respective predictor variable based on hierarchical partitioning. Colour denotes the direction of the relationship: black = positive; white = negative; grey = neutral (based on the unconditional 95% CIs). Abbreviations: LVS - local vegetation structure; PFC - primary forest cover; SFC1 - initial secondary forest cover; SFC2 - intermediate secondary forest cover; SFC3 - advanced secondary forest cover; ED -

edge density; PD - patch density; MNND - mean nearest neighbour distance; MSI - mean shape index. Vertical dotted lines separate vegetation structure, compositional and configurational metrics. See Table S4 and S5 in the Online Supplementary Material for additional modelling results.

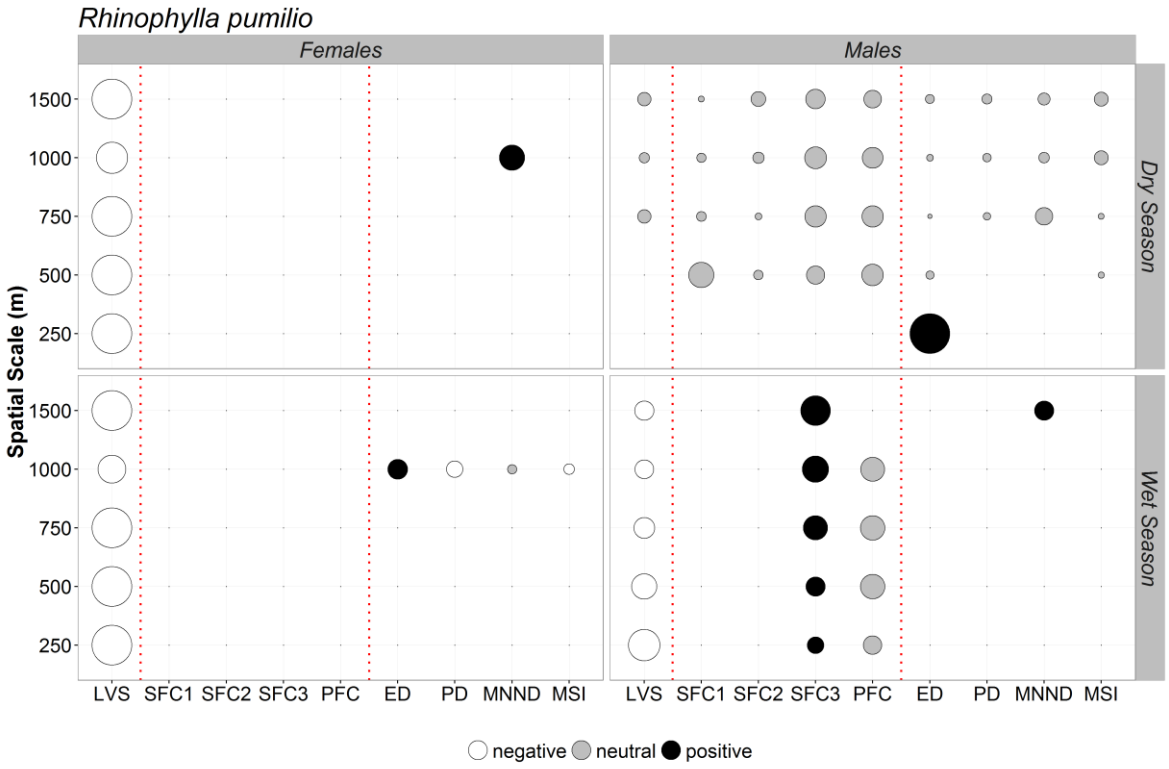

FIGURE 4. Summary results of model averaging of the best-fit generalized linear mixed models (Akaike differences < 2 from the best model) exploring the association between local and landscape-scale predictors and the abundance of male and female *Rhinophylla pumilio* at five focal scales across the Biological Dynamics of Forest Fragments Project. Symbol size is proportional to the variation explained by the respective predictor variable based on hierarchical partitioning. Colour denotes the direction of the relationship: black = positive; white = negative; grey = neutral (based on the unconditional 95% CIs). Abbreviations: see legend to Figure 3. See Table S4 and S5 in the Online Supplementary Material for additional modelling results.

DISCUSSION

Despite the ‘‘soft’’ matrix composed of advanced (> 16 year-old) secondary vegetation and the relatively small distance to continuous forest (80–650 m), bats at the BDFFP exhibit pronounced assemblage- and ensemble-level responses to interior-edge-matrix fragmentation gradients and local and landscape-scale attributes (Rocha *et al.* 2017). These responses reflect strong environmental filters that selectively benefit species with specific functional traits associated with reduced fragmentation sensitivity (Farneda *et al.* 2015) and that are modulated by seasonal fluctuations in resource availability (Ferreira *et al.* 2017). Here, we show that in addition to being trait-mediated and season-modulated, fragmentation responses at the BDFFP are sex-specific for at least three of the locally most abundant bat species, *C. perspicillata*, *R. pumilio* and *P. parnellii*.

Female-male responses to the interior-edge-matrix gradient

Significant differences in the response of female and male bats based on multiple pairwise comparisons were limited to the three most abundant species (*C. perspicillata*, *P. parnellii* and *R. pumilio*). Sex-related differences in habitat use by the other five analysed species were less clear, yet, this might relate to the low number of captures.

Capture rates of *C. perspicillata*, the most abundant phyllostomid species at the BDFFP, were higher for females than males during the dry season at edges and matrix sites and, to a lesser extent, in continuous forest and fragment interiors. During the reproductive period, female bats face higher energetic demands than males (Barclay 1991) and, for *C. perspicillata* the pregnancy peak occurs during the dry season whereas lactation peaks during the wet season

(Bernard 2002, Durant *et al.* 2013, Rocha *et al*. unpublished). To compensate for increased energetic demands, females might forage preferentially in the most resource-rich areas (Barclay 1991, Encarnação 2005), especially in the dry season during which fruit availability is lower (Ramos Pereira *et al.* 2010). Since early successional gap species of the genus *Piper*, the preferred food resource of *C. perspicillata* (Horsley *et al.* 2015), produce two to ten times more fruits than shade tolerant or late successional forest species (Thies & Kalko 2004), the greater proportion of females in edge and matrix habitats, might reflect a shift in the foraging activities of pregnant females to more productive areas. Additionally, *Cecropia* and *Vismia* spp., whose fruits are also favoured by *C. perspicillata* (Horsley *et al.* 2015), are abundant in the secondary forest matrix at the BDFFP (Bentos *et al.* 2008) further justifying the more accentuated female-biased sex-ratios at edges and matrix sites. *Piper*, *Cecropia* and *Vismia* fruits are nutritionally poor and thus bats that rely on these genera have to consume large fruit quantities to meet their dietary needs (Fleming 1986). Augmented capture rates of female *C. perspicillata* in late successional forest during the peak pregnancy period, might therefore reflect increased foraging movements associated with higher energetic demands.

Rhinophylla pumilio, similarly to *C. perspicillata*, belongs to the subfamily Carolliinae and is one of the most locally abundant bat species across the Amazon (Rinehart & Kunz 2006). The species' diet is highly variable but consists primarily of small-seeded understory and mid-canopy fruits of several pioneer plants including *Vismia*, *Piper* and *Cecropia* spp. (Rinehart & Kunz 2006, Horsley *et al.* 2015). At the BDFFP peak pregnancy occurs during the dry season (Bernard 2002, Rocha *et al*. unpublished) and during this season the capture rate of females was nearly three times higher than for males at *Vismia* and *Cecropia*-dominated edge and matrix sites. In the latter habitat, the sex ratio was also female-biased

during the wet season. Since the wet season corresponds to the period of greatest lactation activity for *R. pumilio* at the BDFFP (Bernard 2002) higher female capture rates might relate to increased foraging movements into resource-rich secondary forest areas to compensate the energetic burden associated with milk production.

The capture rate of the high duty-cycle insectivorous bat *P. parnellii* was female-biased in continuous forest and fragments during the wet season and at edges during both the wet and dry seasons. The difference between male and female captures was especially pronounced in the latter habitats, with nearly twice and four times as many females than males in the dry and wet season, respectively. In our study area, the species' pregnancy and lactation peaks occur during the wet and dry seasons, respectively (Rocha *et al.* unpublished). Amazonian populations of *P. parnellii* exhibit greater activity in more cluttered habitats, which also have higher insect biomass (de Oliveira *et al.* 2015). Vegetation structure at edges is characterised by a higher density of pioneer trees and woody lianas (Laurance *et al.* 2006, Faria *et al.* 2009). The species' echolocation, characterized by long constant frequency signals that are well-suited for efficient prey detection in cluttered habitats, might allow females to explore productive foraging areas near edge habitats (Hiryu *et al.* 2016). Male exclusion from more favourable foraging areas is suggested to constitute an important driver of sexual segregation in bats (Senior *et al.* 2005). The near absence of males in this habitat might relate to intraspecific competition for access to prey-rich areas, with females being dominant over males.

Male-female responses to the influence of local and landscape-scale variables

Females and males of both *C. perspicillata* and *R. pumilio* demonstrated discernible differences in their response to local-scale vegetation structure and landscape composition and configuration, as indicated by the results of model consistency between sexes. Similarity of male-female responses was lower for the dry season, the period of peak pregnancy for both species at the BDFFP (Bernard 2002).

During the dry season, compositional metrics were the best predictors of both male and female responses of *C. perspicillata*. However, while the responses of females were characterized by a strong negative influence of PFC across all sampled scales, male responses to PFC were negative at smaller scales (≤ 500 m) but were then substituted by a positive response to SFC3 forest at larger scales. These results show that females clearly favour the pioneer-rich secondary forests during the peak pregnancy period and that males, while equally favouring matrix habitats, tend to select areas close to late-stage successional forest. Telemetry observations from the Atlantic forest show that *C. perspicillata*, while preferentially foraging in early successional forests, preferably roosts in later successional habitats (Trevelin *et al.* 2013). Male preference for sites with higher cover of late-stage secondary forest might thus relate to increased chances of female encounters as they return to their roosts or to roost defence.

Responses of *R. pumilio* females were nearly exclusively related with LVS, whereby the association was consistently negative across all scales examined and during both the dry and wet seasons. Since LVS corresponds to PCA1 (see Fig. S2 and Table S3 of the previous chapter) which reflects a gradient from simpler vegetation structural complexity,

characteristic of secondary forest (greater density of *Vismia* spp. and *Cecropia* spp. trees and woody stems; negative values), to higher structural complexity, characteristic of primary forest sites (more closed canopy cover and greater density of trees; positive values), a negative association with LVS means that more cluttered habitats are avoided. This negative association with LSV, although also found for male bats in the wet season, was not so marked. Due to its small body size and low aspect ratio and associated relative wing loading, *R. pumilio* (~9 g) incurs higher flight costs compared to larger fruit-eating bats (Speakman & Thomas 2003, Marinello & Bernard 2014). Since flying in cluttered habitats is more energy demanding than flying in more open areas (Grodzinski *et al.* 2009), the elevated energetic costs associated with higher vegetation complexity might represent a particularly high burden for female bats during both pregnancy (dry season) and while nursing (wet season). During lactation, these energetic costs might be further amplified due to the transportation of their young since female *R. pumilio* often transport their pups to temporary night roosts across their foraging area (Henry & Kalko 2007).

The results of this study align with previous findings from temperate areas, in which male and female bats differed in their responses to local and landscape-scale metrics of habitat quality, composition and configuration in an urban setting (Lintott *et al.* 2014). They also agree with several telemetry studies providing evidence for gender-specific differences in habitat use in Neotropical bats (*e.g.* Meyer *et al.* 2005, Henry & Kalko 2007, Albrecht *et al.* 2007). Yet, they contrast with recent findings from humanized forest landscapes in Costa Rica for which no sex differences in habitat use were observed (Frank *et al.* 2016).

Conclusions

Our results suggest that, at least for some species, male and female bats respond to fragmentation in different ways and that responses to local- and landscape-scale attributes are sex- and season-specific. This has considerable implications for our understanding of how tropical species adapt to human-induced habitat changes as modifications in population structure (sex-ratio) can act to diminish or magnify the pervasive consequences of forest loss, fragmentation and deterioration.

ACKNOWLEDGMENTS

We would like to thank the multitude of volunteers and field assistants that helped collecting data, the coordination team of the BDFFP and Paulo E.D. Bobrowiec for logistic support and Tobias Jeppsson for providing a modified version of the hier.part function for the hierarchical partitioning analysis. Funding was provided by the Portuguese Foundation for Science and Technology to C.F.J.M. (PTDC/BIA-BIC/111184/2009), R.R. (SFRH/BD/80488/2011) and A.L.-B. (PD/BD/52597/2014). J.M.B.C was funded as part of NERC's support of the National Centre for Earth Observation. This research was conducted under ICMBio permit (26877-2) and constitutes publication number XXX of the BDFFP technical series.

Online Supplementary Material can be found at:

http://www.r-rocha.com/wp-content/uploads/2015/09/Supplementary-Material-PhD-thesis-Ricardo-Rocha-Chapter-3.pdf

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Supplementary Material

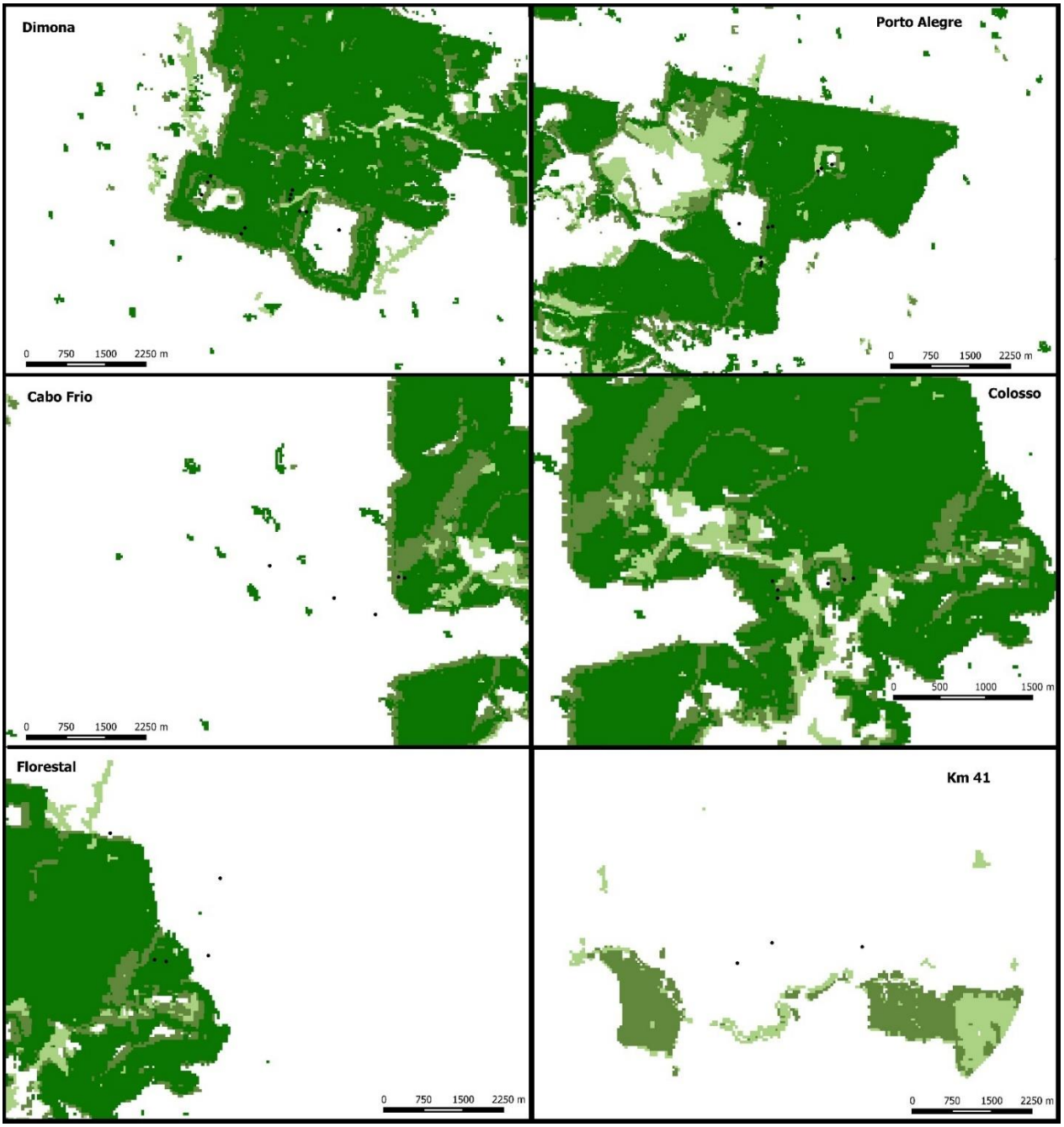

FIGURE S1. Map showing the distribution of the different successional stages of secondary forest around each fragment and reserve in the Biological Dynamics of Forest Fragments Project (BDFFP) study area, in the central Amazon. White represents primary forest cover and different shades of green (from light to dark) the different secondary forest cover (SFC) age classes (initial (≤ 5 years) – SFC1; intermediate (6-15 years – SFC2); advanced (≥ 16 years) – SFC3); The black dots represent the sampling sites.

TABLE S1. Number of adult bats captured for each phyllostomid bat species and *Pteronotus parnellii* sampled in the BDFFP. Central Amazon. Brazil. Ensemble abbreviations: GLAN = Gleaning animalivore; FRUG = frugivore (C = canopy and S = shub); NECT = nectarivore; SANG = sanguivore. Species analysed are highlighted in bold.

		Females / Males								
		Dry Season				**Wet Season**				
Taxon	**Ensemble**	**Cont. Forest**	**Frag.**	**Edge**	**Matrix**	**Cont. Forest**	**Frag.**	**Edge**	**Matrix**	**Total**
Phyllostomidae										
Ametrida centurio	FRUG (C)	2 / 0	0 / 0	2 / 2	2 / 0	0 / 0	0 / 0	0 / 0	0 / 1	6 / 3
Anoura caudifer	NECT	0 / 0	0 / 0	0 / 1	0 / 0	0 / 1	0 / 1	0 / 1	1 / 0	1 / 4
Artibeus cinereus	FRUG (C)	3 / 3	0 / 1	4 / 1	5 / 1	2 / 3	2 / 1	0 / 1	1 / 1	17 / 12
Artibeus concolor	FRUG (C)	0 / 0	6 / 1	14 / 4	21 / 14	0 / 1	1 / 0	0 / 1	1 / 0	43 / 21
Artibeus gnomus	FRUG (C)	2 / 2	0 / 2	5 / 1	1 / 2	2 / 3	1 / 1	4 / 1	4 / 5	19 / 17
Artibeus lituratus	FRUG (C)	10 / 2	3 / 1	2 / 2	17 / 2	5 / 4	1 / 0	0 / 0	0 / 0	38 / 11
Artibeus obscurus	**FRUG (C)**	**4 / 5**	**9 / 2**	**31 / 9**	**31 / 14**	**5 / 7**	**7 / 5**	**3 / 0**	**1 / 3**	**82 / 45**
Artibeus planirostris	FRUG (C)	4 / 0	4 / 0	0 / 1	0 / 0	3 / 2	2 / 1	0 / 0	2 / 0	15 / 4
Carollia brevicauda	**FRUG (S)**	**2 / 3**	**6 / 1**	**4 / 3**	**4 / 6**	**6 / 6**	**9 / 6**	**17 / 12**	**18 / 17**	**67 / 54**
Carollia castanea	FRUG (S)	0 / 0	3 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	3 / 0
Carollia perspicillata	**FRUG (S)**	**42 / 39**	**183 / 108**	**116 / 59**	**116 / 74**	**65 / 45**	**117 / 90**	**169 / 124**	**180 / 156**	**1022 / 695**
Choeroniscus minor	NECT	0 / 0	3 / 1	0 / 0	0 / 0	1 / 0	2 / 0	0 / 0	0 / 0	6 / 1
Chrotopterus auritus	GLAN	0 / 1	2 / 0	0 / 0	0 / 0	0 / 2	0 / 0	0 / 0	0 / 0	2 / 3
Desmodus rotundus	SANG	1 / 1	0 / 0	0 / 0	0 /1	3 / 0	1 / 0	0 / 1	0 / 0	5 / 3
Glossophaga soricina	NECT	0 / 0	0 / 3	0 /1	0 / 0	1 / 1	1 / 1	0 / 0	0 / 0	2 / 6
Glyphonycteris daviesi	GLAN	1 / 0	0 / 0	0 / 0	0 / 0	1 / 1	0 / 0	0 / 0	1 / 1	3 / 2
Glyphonycteris sylvestris	GLAN	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 1
Lampronycteris brachyotis	GLAN	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	1 / 0
Lonchophylla thomasi	NECT	1 / 6	2 / 4	0 / 0	1 / 1	4 / 1	5 / 5	2 / 1	0 / 0	15 / 19

Lophostoma brasiliense	GLAN	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	3 / 0	0 / 0	3 / 1
Lophostoma carrikeri	GLAN	1 / 0	0 / 1	1 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	2 / 3
Lophostoma schulzi	GLAN	1 / 1	0 / 1	0 / 0	0 / 0	0 / 2	0 / 1	1 / 0	0 / 2	2 / 7
Lophostoma silvicolum	**GLAN**	**10 / 11**	**4 / 3**	**1 / 1**	**2 / 1**	**14 / 10**	**5 / 2**	**5 / 5**	**3 / 3**	**44 / 36**
Mesophylla macconnelli	FRUG (C)	5 / 3	0 / 1	0 / 1	0 / 0	2 / 2	0 / 3	1 / 1	0 / 1	8 / 12
Micronycteris hirsuta	GLAN	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	1 / 1
Micronycteris megalotis	GLAN	1 / 0	1 / 0	0 / 0	0 / 1	0 / 0	0 / 0	1 / 0	0 / 0	3 / 1
Micronycteris microtis	GLAN	0 / 2	1 / 0	0 / 0	0 / 0	2 / 1	0 / 2	1 / 0	3/ 0	8 / 5
Micronycteris schmidtorum	GLAN	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1
Mimon crenulatum	**GLAN**	**10 / 8**	**2 / 3**	**2 / 3**	**4 / 3**	**1 / 5**	**5 / 5**	**9 / 11**	**6 / 10**	**39 / 48**
Phylloderma stenops	GLAN	0 / 1	1 / 2	0 / 0	1 / 0	2 / 4	0 / 0	2 / 1	1 / 1	7 / 9
Phyllostomus discolor	NECT	2 / 0	2 / 0	1 / 0	0 / 0	0 / 1	0 / 0	1 / 1	0 / 1	6 / 3
Phyllostomus elongatus	GLAN	6 / 10	2 / 1	0 / 1	0 / 0	0 / 3	2 / 1	1 / 2	1 / 0	12 / 18
Phyllostomus hastatus	GLAN	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	0 / 0	0 / 0	1 / 0
Platyrrhinus helleri	FRUG (C)	0 / 0	0 / 0	1 / 1	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	2 / 1
Rhinophylla pumilio	**FRUG (S)**	**31 / 18**	**57 / 21**	**22 / 7**	**24 / 6**	**23 / 15**	**38 / 15**	**44 / 30**	**48 / 20**	**287 / 132**
Sturnira tildae	FRUG (S)	0 / 1	1 / 0	1 / 0	5 / 1	0 / 0	1 / 0	4 / 0	7 / 4	19 / 6
Tonatia saurophila	GLAN	2 / 5	2 / 6	1 / 0	0 / 1	10 / 10	5 / 6	3 / 1	1 / 2	24 / 31
Trachops cirrhosus	**GLAN**	**14 / 8**	**1 / 5**	**2 / 2**	**2 / 0**	**23 / 14**	**12 / 9**	**2 / 2**	**6 / 7**	**62 / 47**
Trinycteris nicefori	GLAN	1 / 1	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 2	0 / 2	1 / 6
Uroderma bilobatum	FRUG (C)	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1 / 0	1 / 0
Vampyressa pusilla	FRUG (C)	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 1	0 / 0	0 / 1
Vampyriscus bidens	FRUG (C)	3 / 0	1 / 2	0 / 0	0 / 1	0 / 7	1 / 1	1 / 0	1 / 1	7 / 12
Vampyriscus brocki	FRUG (C)	0 / 0	0 / 1	0 / 0	0 / 0	0 / 0	1 / 0	1 / 0	0 / 0	2 / 1
Mormoopidae										
Pteronotus parnellii	**AEIN**	**40 / 5**	**23 / 14**	**10 / 1**	**14 / 2**	**64 / 4**	**9 / 4**	**24 / 10**	**25 / 11**	**209 / 51**
Total captures		239/136	319/187	200/103	251/131	239/157	230/161	299/209	320/250	2097/1334

TABLE S2. Results of likelihood ratio tests for differences in the abundance of each species between sexes (male and female) and habitat types (interior. edge and matrix) for both seasons (dry and wet). Significant (adjusted P < 0.05) results are highlighted in bold.

	Gender			Gender x Season			Dry Season (Gender x Habitat Type)			Wet Season (Gender x Habitat Type)		
Species	**Pr(>Chisq)**	**Chisq**	**Df**	**Pr(>Chisq)**	**Chisq**	**Df**	**Pr(>Chisq)**	**Chisq**	**Df**	**Pr(>Chisq)**	**Chisq**	**Df**
Artibeus obscurus	**09424**	10.937	1	**< 2.2e-16**	91.595	3	**0.005059**	20.247	7	0.1129	11.645	7
Carollia brevicauda	0.2368	1.399	1	**0.01373**	10.658	3	**0.04168**	14.587	7	0.1799	10.156	7
Carollia perspicillata	**2.458e-15**	62.659	1	**< 2.2e-16**	95.813	3	**4.30e-13**	72.651	7	**7.345e-05**	30.607	7
Lophostoma silvicolum	0.3707	0.801	1	0.7738	1.114	3	**0.00111**	24.065	7	**06376**	25.425	7
Mimon crenulatum	0.3342	0.933	1	0.5762	1.982	3	**0.02467**	16.049	7	0.3308	8.02	7
Pteronotus parnellii	**< 2.2e-16**	103.02	1	**< 2.2e-16**	117.19	3	**1.52e-06**	39.57	7	**< 2.2e-16**	125.78	7
Rhinophylla pumilio	**1.814e-14**	58.724	1	**2.021e-13**	62.17	3	**1.03e-09**	55.801	7	**3.29e-09**	53.263	7
Trachops cirrhosus	0.1501	2.071	1	**5.514e-05**	22.351	3	0.4134	7.15	7	**0.01975**	16.657	7

CHAPTER 4

Design matters: an evaluation of the impact of small man-made forest clearings on tropical bats using a before-after-control-impact design

Rocha, R., Ovaskainen, O., López-Baucells, A., Farneda, F.Z., Ferreira, D., Bobrowiec. P.E.D., Palmeirim, J.M. & Meyer, C.F.J. Design matters: an evaluation of the impact of small forest clearings on tropical bats using a before-after-control-impact design. *Submitted.*

CHAPTER 4

Design matters: an evaluation of the impact of small man-made forest clearings on tropical bats using a before-after-control-impact design

ABSTRACT

In recent years, large clearings (> 1000 ha) accounted for gradually smaller amounts of total annual deforestation in the Brazilian Amazon, whereas the proportion of small clearings (< 50 ha) nowadays represents more than 80% of annual deforestation. Despite the ubiquity of small clearings in fragmented Amazonian landscapes, most fragmentation research has focused on the effects of large-scale deforestation, leading to a poor understanding of the impacts of smaller barriers on Amazonian vertebrates. We capitalized on the periodical re-isolation of experimental forest fragments at the Biological Dynamics of Forest Fragments Project in the Central Amazon as a before-after-control-impact experiment to investigate the short-term effects of small clearings on bat assemblages. Over the course of three years we sampled six control sites in continuous forest, the interiors and edges of eight forest fragments as well as eight sites in the surrounding matrix. Sampling took place both before and after the experimental manipulation (clearing of a 100 m wide strip of regrowth around each fragment), resulting in ~6 000 bat captures. Species were classified as old-growth specialists and habitat generalists according to their habitat affinities and a joint species distribution modelling framework was used to investigate the effect of fragment re-isolation on species occupancy. Following fragment re-isolation, species richness declined in all habitats other than fragment edges and, although responses were idiosyncratic, this decline was more pronounced for forest specialist than for generalist species. Additionally, fragment re-

isolation led to a reduction in the similarity between assemblages in modified habitats (fragment interiors, edges and matrix) and continuous forest. Sampling of controls in continuous forest both prior to and after re-isolation revealed that much of the variation in bat species occupancy between sampling periods did not arise from fragment re-isolation but rather reflected natural spatiotemporal variability. This emphasizes the need to sample experimental controls both before and after experimental manipulation and suggests caution in the interpretation of results from studies in which the effects of habitat transformations are assessed based solely on data collected using space-for-time substitution approaches.

Key-words: Amazon, BACI, Bayesian inference, fragmentation, hierarchical modelling, joint species distribution modelling.

1. Introduction

Human reshaping of natural ecosystems has unleashed one of the greatest biodiversity crises the planet has ever faced (Ceballos et al., 2015; Newbold et al., 2016). Habitat loss and fragmentation are among the primary causes of this global demise (Haddad et al., 2015) and their impact is especially worrisome in tropical forests, the most diverse and complex terrestrial ecosystems (Bradshaw et al., 2008; Hansen et al., 2013). A better understanding of the patterns and processes associated with the division of continuous forest into smaller and more isolated fragments is thus critical for the implementation of management programs aimed at abating the ongoing biotic homogenization of wildlife assemblages that persist in fragmented human-altered tropical landscapes.

With an area of ~5.3 million km^2 the Amazon forest is the dominant biome in the Neotropics and the largest block of rainforest remaining on Earth (Aragão et al., 2014). Around 60% of this area is located within Brazil and although much of it still constitutes mostly undisturbed evergreen rainforest, the expansion of agricultural activities, logging, ground fires and urbanization have reduced forest cover at an average annual rate of 19,500 km^2 between 1996 and 2005 (Nepstad et al., 2009). By 2013 this figure was 5,843 km^2, representing a 70% decrease in the rate of deforestation (Nepstad et al., 2014). Over recent years, large clearings (>1,000 ha) have accounted for gradually lesser extents of total annual deforestation, whereas the proportion of small clearings (6.25–50 ha) has remained unchanged and nowadays represents more than 80% of annual deforestation (Rosa et al., 2012). Despite this prevalence of small clearings in the Brazilian Amazon and elsewhere in the tropics, most research on forest disturbance has focused on large-scale deforestation, leading to a poor understanding of the impacts of smaller barriers on tropical wildlife (Laurance et al., 2009).

Although observational studies have offered valuable insights into the effects of anthropogenic disturbances on tropical species (e.g. Laurance et al., 2004; Avila-Cabadilla et al., 2009; Rocha et al., 2015), they are typically hampered by the absence of rigorous controls, insufficient replication and lack of baseline data (Ramage et al., 2013; Bicknell et al., 2015; Meyer et al., 2016). Whole-ecosystem fragmentation experiments can overcome some of these drawbacks, offering an opportunity to assess the effects of small man-made clearings on fragment assemblages using before-after-control-impact (BACI) sampling, a potent experimental design in which replicates of treatments and controls are surveyed both prior to and after manipulation (Fayle et al., 2015). This allows for stronger inference than studies that analyse chronosequences and depend on a space-for-time substitution approach (Block et al., 2001; França et al., 2016).

The Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon is the world's largest and longest-running experimental study of forest fragmentation (Haddad et al., 2015). Forest fragments at the BDFFP were isolated from continuous forest by distances of 70-1000 m in the early 1980s. However, due to secondary regrowth, fragment isolation has been maintained ever since by the clearing of a 100 m wide strip of secondary vegetation around each fragment. This re-isolation takes place at intervals of ~10 years (Laurance et al., 2011) (Fig. 1). The areas of secondary forest cleared around the BDFFP forest fragments range from 6.4 to 42 ha and thus accurately mirror current patterns of deforestation in the Brazilian Amazon (Rosa et al., 2012).

Bats are the second most diverse mammalian order with over 1300 recognized species (Fenton and Simmons, 2015). They reach their highest richness in the Neotropics (Altringham, 2011), where they provide key ecological services such as seed dispersal, pollination, and regulation of small vertebrate and invertebrate populations (Kunz et al., 2011). They are sensitive to land-use change (García-Morales et al., 2013; Meyer et al., 2016), a feature that, in combination with their high abundance, richness, ecological diversity and relative ease of survey, qualifies them as a good model taxon for investigating the impacts of forest disturbance (Jones et al., 2009).

Species vary widely in their sensitivity to forest disturbance, depending on their habitat affinities and species-specific characteristics (Newbold et al., 2013; Farneda et al., 2015). However, the assessment of faunal responses to forest disturbance is often based on composite biodiversity metrics that may conceal species-level responses and consequently misguide conservation actions and management (Klingbeil and Willig, 2009). The reliance on such metrics often is a consequence of the rarity of old-growth specialist species for which limited data prevents sufficient statistical power for species-specific approaches. Here, we capitalize on the periodical re-isolation of the BDFFP

fragments as a BACI experiment to investigate how abrupt changes in fragment-matrix contrast affect Neotropical bats. We use a joint species distribution modelling framework that combines species-specific models into a single hierarchical model thus allowing the assessment of the influence of environmental variables at the level of individual species regardless of their rarity within the assemblage (Ovaskainen et al., 2016a). By combining species-level inference with a robust sampling design, in which surveys in modified habitats as well as in undisturbed reference sites in continuous forest were conducted prior to and following the impact of re-isolation, we were capable of unveiling, for the first time, the short-term effects of the creation of small clearings on tropical bats at both the species and assemblage levels.

We hypothesized that fragment re-isolation would reduce species occupancy in fragments and adjoining edge and matrix sites and lead to a decrease in similarity between the assemblages inhabiting these habitats and the ones found in nearby continuous forest (used as experimental controls). We predicted that following fragment re-isolation: i) the reduction in occupancy would be more marked for species classified as old-growth specialists than for habitat generalists; ii) species responses would be idiosyncratic, with re-isolation effects being more prominent in edge and matrix habitats than in fragment interiors and iii) the assemblage similarity between continuous forest and edge and matrix sites would decrease more than the assemblage similarity between continuous forest and fragment interiors.

2. Materials and methods

2.1. Study area

The study was conducted at the BDFFP, situated about 80 km north of Manaus (2°30'S, 60°W), Amazonas, Brazil. The area comprises c. 40 x 10 km of a mosaic of *terra firme* rainforest, secondary regrowth, and primary forest fragments and lies 30–125 m a.s.l. The area is characterized by elevated tree species richness (often exceeding 280 species ha-1) (Oliveira and Mori, 1999) and rainfall varies from 1,900 to 3,500 mm annually, with a dry season between June and October (Laurance et al., 2011). Fragments used in this study were isolated from continuous forest by distances of 80-650 m in the early 1980s, and are 1, 10 and 100 ha in size. The landscape matrix is composed of ~20-year-old secondary forest dominated mainly by *Vismia* spp. and *Cecropia* spp. (Mesquita et al., 2015).

2.2. Fragment re-isolation

Following the initial isolation of the fragments in the early 1980s secondary forest has occupied much of the areas previously cleared. Fragment isolation was thus maintained by clearing and burning of a 100 m wide strip of regrowth around each of the forest fragments at intervals of ~10 years, prior to this study most recently between 1999 and 2001 (Laurance et al., 2011). Fragment re-isolation took place again between November 2013 and March 2014, by clearing (but not burning) of areas ranging from 6.4 (around 1 ha fragments) to 42 ha (around 100 ha fragments) around each of the experimental forest fragments (Fig. 1 and Fig. S1). During the above-mentioned periods no manipulation took place in the nearby continuous forest, which were used as experimental controls.

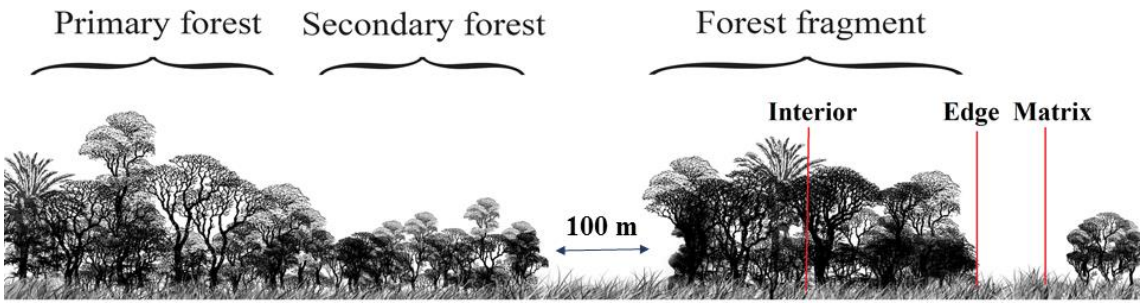

Figure 1 – Schematic representation of the sampling design after the experimental re-isolation of fragments by clearing of the surrounding regrowth vegetation.

2.3. Bat sampling

Field work before and after re-isolation was conducted from August 2011 to June 2013 and from April to November 2014, respectively. The bat fauna was sampled in eight forest fragments, categorized according to their area as "1 ha" (n = 3), "10 ha" (n = 3) and "100 ha" (n = 2) and six control sites in continuous forest (CF). Fragments were located at different BDFFP camps (Dimona, Colosso and Porto Alegre), whereas CF interior sites were located in Cabo Frio and Km 41. Mist net sampling was performed in the interiors and at the edges of all fragments, as well as in sites located 100 m away from the edge of each fragment, in the adjacent secondary regrowth. The latter, referred to hereafter as "matrix sites", were located at the border of the area of secondary regrowth cleared during the re-isolation of the fragments. At fragment edges, mist nets were deployed parallel to the border between the fragment and the adjoining matrix (Fig. 1).

At each site, bats were sampled eight times before fragment re-isolation (four times in each season) and four times after fragment re-isolation (twice per season). Fourteen ground-level mist nets (12 x 2.5 m, 16 mm mesh, ECOTONE, Poland) were used in CF and fragment interiors and seven at edge and matrix sites. Nets were opened at dusk and

were deployed for six hours, being revised at intervals of ~20 minutes. Total mist net effort was 6046, 8025, 3994 and 4005 mist-net hours (mnh; 1 mnh equals one 12 m net open for 1 h) for continuous forest, fragment interior, edge and matrix, respectively. Bias in capture rates due to net shyness was avoided by spacing visits to the same site by periods of three to four weeks (Marques et al., 2013). Species were identified following Lim and Engstrom (2001) and Gardner (2007), and taxonomy follows Gardner (2007).

With the exception of the mormoopid bat *Pteronotus parnellii* we excluded all non-phyllostomid species from the analysis as they cannot be adequately sampled with mist-nets (Kalko, 1998).

2.4. Classification of species habitat affinities

Bat captures from this and previous studies at the BDFFP (Sampaio, 2001; Bobrowiec and Gribel, 2010; Rocha et al., 2017) were compiled into a database amounting to 10,311 captures of 50 species sampled in the understory of CF, fragments and secondary forest across the BDFFP landscape between 1996 and 2014. The joint species distribution model (see below) was only based on a sub-set of these captures (4,244 individuals from 47 species). Captures were divided into two categories, namely: CF *vs* forest fragments and secondary forest. Species were then classified according to their habitat affinity into CF specialists, secondary forest specialists, generalists or too rare to classify using the statistical approach described in Chazdon et al. (2011). Classification was conducted in R v.3.0.2 (R Development Core Team, 2013) using the *vegan* package and setting a significance level of $P = 0.01$. We conservatively grouped CF specialists and species too rare to classify into a single group and since only two species were assigned to the secondary forest category, they were lumped together with generalists. We therefore

considered two groups according to their habitat affinity in our analysis: CF specialists and species too rare to classify (hereafter "specialist species") and generalists and secondary forest specialists (hereafter "generalist species").

2.5. Hierarchical joint species distribution model

We evaluated the effect of fragment re-isolation by means of a hierarchical joint species distribution model (Ovaskainen and Soininen, 2011; Warton et al., 2015; Ovaskainen et al., 2016a, b). For the analyses we considered one mist-netting session in one sampling site (n = 360 mist-netting sessions) as a sampling unit. Due to the high prevalence of zeros in the data, we truncated the counts to presence-absence, and thus considered as the response variable the vector of presence-absences of all the 50 species. We assumed a Bernoulli distribution with probit link function. Explanatory variables were: i) habitat type (categorical: CF, fragment interior, fragment edge or matrix); ii) survey period (categorical: before or after re-isolation); iii) percentage of primary forest cover within a radius of 500 m from each site; and iv) log-transformed survey effort. We also included an interaction between survey period and habitat type. Percent primary forest cover at each sampling site was calculated based on a detailed vegetation map of the BDFFP derived from Landsat Thematic Mapper data from 2011 - see Carreiras et al. (2014) for image classification details - and a 500 m buffer scale was selected to avoid overlap between neighbouring sites. Multiple visits to the same site were accounted for by including a site-level random effect in the model, implemented at the community level using a latent factor approach (Ovaskainen et al., 2016a). The species habitat affinity classification described above was included as a trait and phylogenetic non-independence was accounted for by structuring the error variance with a phylogenetic correlation matrix

derived from a phylogenetic tree under the diffusion model, following Abrego et al. (2017). The phylogenetic tree was extracted from Jones et al. (2002) and we fitted the model in the Bayesian framework using the Gibbs sampler of Ovaskainen et al. (2016a, b).

The parameterized model was used to predict the expected mean species richness before and after fragment re-isolation for all species and separately for generalists and specialists. Mean species richness was defined as the model prediction for the number of species expected to be observed during a survey visit and computed as the sum (over the species) of the species-specific occurrence probabilities. Predictions were based on mist netting effort standardized to the mean value over all visits and the percentage of primary forest cover standardized to the mean value of a given habitat category.

To examine how fragment re-isolation affected assemblage turnover, we calculated assemblage similarity among the control (CF) and modified habitats (fragment interior, fragment edge and matrix) as the correlation between model-predicted log-transformed occurrence probabilities (Ovaskainen and Soininen, 2011). We performed these analyses for all species and separately for generalists and specialists. The influence of the amount of primary forest cover on assemblage similarity was investigated by assessing the correlation between model estimates based on predictions using the mean (33%), minimum (4%) and maximum (100%) values for the percentage of primary forest cover within a radius of 500 m at each site.

3. Results

Ground-level mist netting led to the capture of 4244 bats (3079 before re-isolation and 1165 after re-isolation) belonging to 47 species. Twenty-seven species were classified as specialists whereas 23 were classified as generalists (Table S1 and Fig. S2).

3.1 Occupancy responses to fragment re-isolation

3.1.1. Changes in species richness

Model predicted numbers of species captured per sampling visit indicated that CF was the most species-rich habitat both before and after experimental manipulation, yet also the one showing the largest declines (5.96 ± 0.78 [mean ± SD] before; 4.86 ± 0.74 after) (Fig. 2). Among the habitats exposed to experimental manipulation, species richness was the highest in fragment interiors (5.01 ± 0.74 before; 4.2 ± 0.69 after), followed by matrix (4.24 ± 0.6 before; 3.48 ± 0.6 after) and edge sites (2.94 ± 0.53 before; 3.32 ± 0.58 after). When separating the species by their habitat affinity, specialists exhibited the same pattern of decreasing species richness from CF to fragment interiors, matrix and edge habitats, however, after fragment re-isolation generalists were more species-rich at edges than in the matrix (Fig. 2).

Overall, species richness was higher before than following fragment re-isolation. This pattern was consistent in CF, fragment interiors and, to a lesser extent, the matrix (18%, 15% and 9% decrease in species richness following fragment re-isolation). The sole exception, though with limited statistical support, were the fragment edges, for which the model estimated a 13% increase in species richness following re-isolation (Fig. 2).

The between-period change in species richness was more pronounced for specialist species than for generalists (Fig. 2). Whereas for generalists the support for a decline in

species richness in any of the considered habitats was low (posterior probability < 95%), old-growth specialist species were significantly less likely to be captured after fragment re-isolation in all habitats, except fragment edges. For the latter, and similarly to generalists, model predictions were higher after fragment re-isolation (7 and 32% increase for generalists and specialists, respectively), however, with no significant differences (Fig. 2).

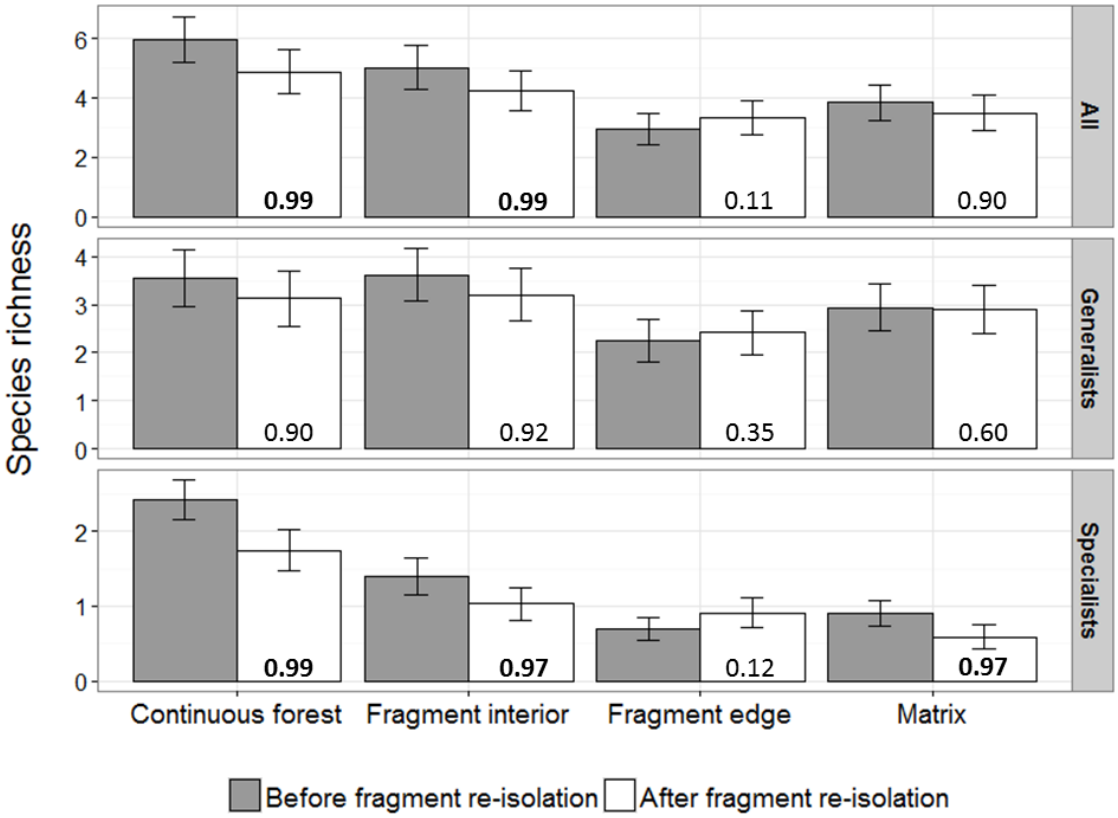

Figure 2 – Patterns of species richness at continuous forest and fragment interior, edge and matrix sites of the Biological Dynamics of Forest Fragments Project before and after fragment re-isolation. Plotted are the predictions for the mean number of species (± posterior standard deviation) expected to be observed during a survey visit for all species combined and separately for generalist and specialist bats. Inserts to the after fragment re-isolation bars represent the posterior probabilities for the predictions being lower after fragment re-isolation than before re-isolation; values showing high statistical support (posterior probability > 95%) are highlighted in bold. The classification of the species into generalists and specialists is reported in Table S1.

3.1.2. Species-specific responses to fragment re-isolation

For both generalists and specialists, more species declined in occupancy than increased following fragment re-isolation (Fig. 3). Model predictions revealed high statistical support (posterior probability > 95%) for the decline in occupancy probability of 13% of the generalist and 19% of the specialist species in CF. The only habitats to exceed CF in the number of species exhibiting significant negative changes were fragment interiors, for which 17% of the generalists and 22% of the specialists exhibited high statistical support for a decrease in occupancy following fragment re-isolation (Fig. 3).

For generalists, the same number of species showed high support for positive and negative changes in occupancy in edge and matrix sites. The same pattern was observed for specialist species in matrix sites, yet for edge sites, 11% of the specialist species exhibited high support for an increase following re-isolation whereas no species had high support for negative changes in occupancy.

For generalists, high support for increases in occupancy was only found for *Artibeus obscurus* in CF, and for *A. concolor* in edge and matrix sites (Fig. 4). The more pronounced declines among generalists were found for *Rhinophylla pumilio* in CF, fragment interiors and matrix, followed by *Tonatia saurophila* in CF and *Lonchophylla thomasi* in fragment interiors. On the other hand, for specialists, high support for positive between-period changes was only found for *Micronycteris sanborni*, *Mesophylla macconnelli* and *Ametrida centurio* in edge, and for *A. centurio*, *Chiroderma trinitatum* and *C. villosum* in matrix sites. For this group, the more significant negative changes were found for *Pteronotus parnellii* and *Trachops cirrhosus* in matrix sites, *T. cirrhosus* in CF and *Phyllostomus elongatus* and *Choeroniscus minor* in fragment interiors (Fig. 4).

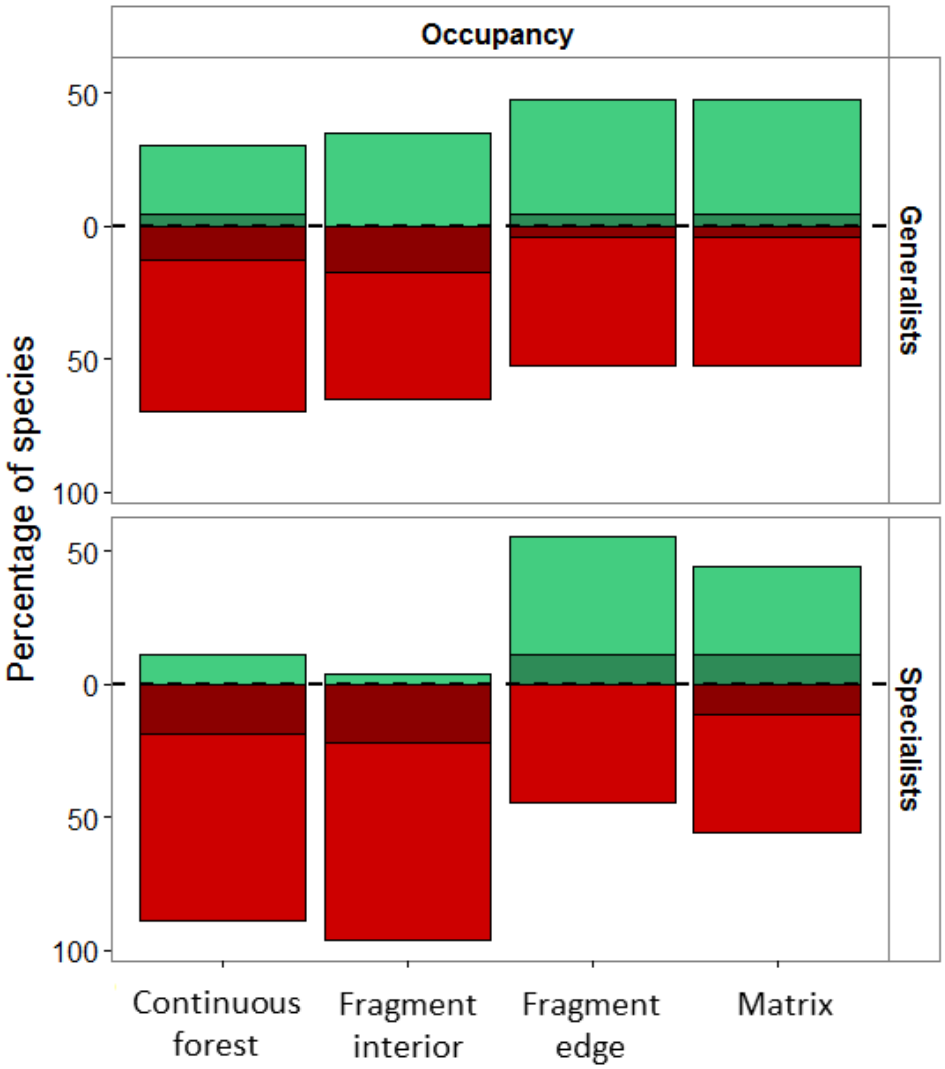

Figure 3 – Percentage of generalist and specialist species with negative (red) and positive (green) changes in occupancy after fragment re-isolation at the Biological Dynamics of Forest Fragments Project. Dark colours represent species with high statistical support (posterior probability > 95%) whereas light colours stand for species with low statistical support (posterior probability < 95%). Predictions account for within-habitat differences in capture effort between the two periods.

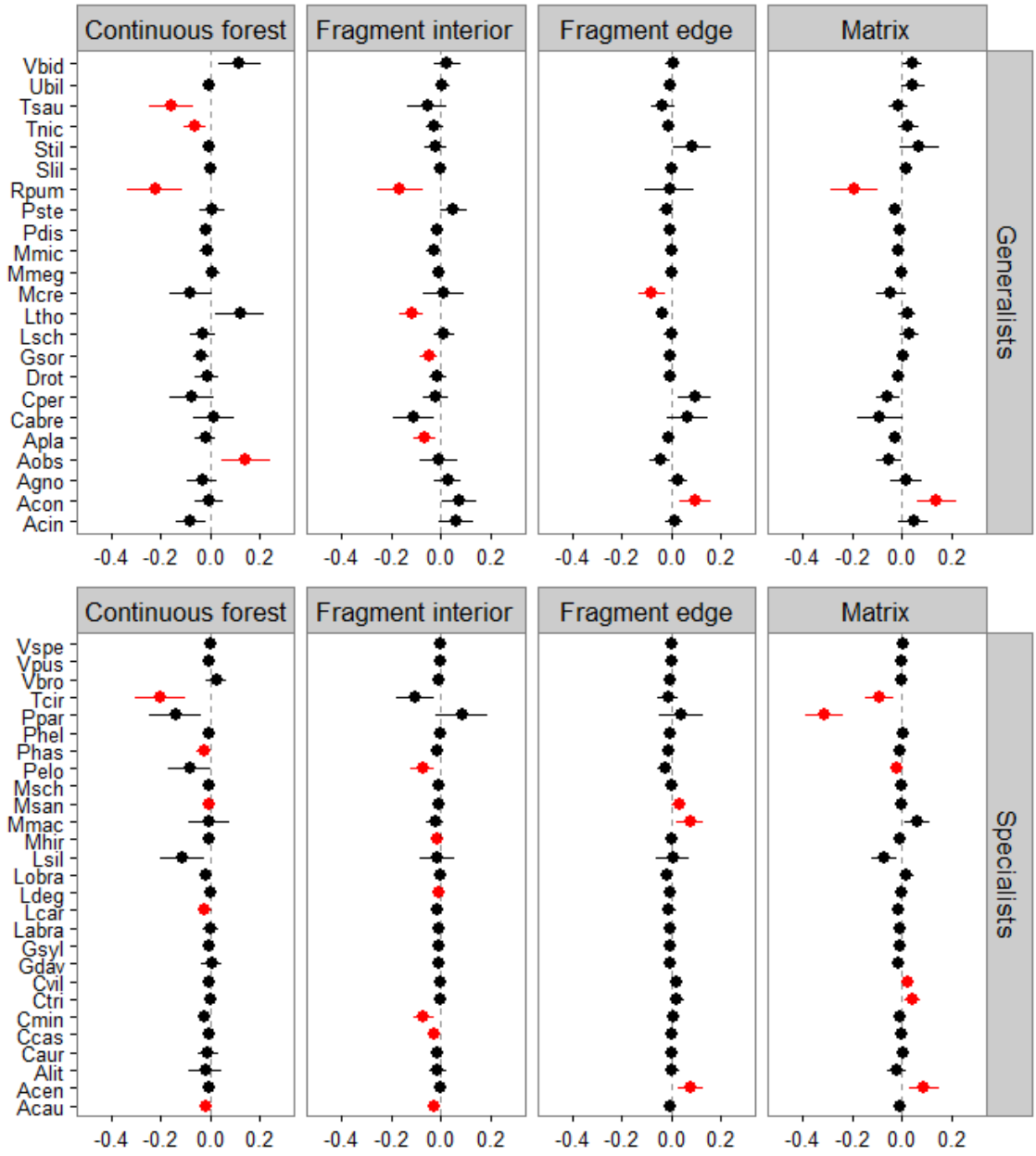

Figure 4 - Changes in species occupancy probability associated with fragment re-isolation of forest generalist and specialist bat species across the different habitat types sampled at the Biological Dynamics of Forest Fragments Project. Plotted are the species-specific differences in the predictions of mean occupancy per survey visit before and after fragment re-isolation (± posterior standard deviation). Species with high statistical support (posterior probability > 95%) are highlighted in red. Species codes are reported in Table S1.

3.2. Changes in assemblage similarity

Model predictions indicate that within-habitat assemblage similarity before and after fragment re-isolation was highest for CF (0.8), followed by fragment interiors (0.74), fragment edges and matrix (0.62) (Table S2).

Assemblage similarity between CF and fragment interiors, edge and matrix decreased following fragment re-isolation. These declines in assemblage similarity were more discernible for specialist than for generalist species and, for both groups, the reduction in assemblage similarity was more pronounced at fragment edges and matrix sites than in fragment interiors (Table 1). Additionally, model predictions based on the minimum and maximum values of forest cover within a 500 m radius indicate that following fragment re-isolation, fragment interiors, edge and matrix sites surrounded by a higher percentage of forest cover experienced a smaller decrease in assemblage similarity relative to CF, than more deforested sites (Table S3).

Table 1 - Assemblage similarity between continuous forest and modified habitats (fragment interiors, fragment edges and matrix sites), before and after fragment re-isolation. We defined the similarity between two assemblages as the correlation between model-predicted occurrence probabilities (log-transformed). The values in the table show posterior mean similarities between assemblages in CF and modified habitats for the two study periods. Values are based on the mean amount of primary forest present within a 500 m buffer centred on each sampling site (see Table S3 for assemblage similarity based on model-predicted occurrence probabilities for low and high values of primary forest cover).

	Fragment interior		**Fragment edge**		**Matrix**	
	Generalists	*Specialists*	*Generalists*	*Specialists*	*Generalists*	*Specialists*
Before re-isolation	0.86	0.79	0.63	0.63	0.60	0.66
After re-isolation	0.72	0.64	0.38	0.28	0.34	0.33
% change[1]	16%	19%	40%	55%	44%	50%
Posterior probability[2]	0.87	0.86	0.94	**0.97**	0.93	**0.97**

[1] Percent change in assemblage similarity before and after fragment re-isolation.

[2] Posterior probability of assemblage similarity being higher before than after fragment re-isolation; values showing high statistical support (posterior probability > 95%) are highlighted in bold.

4. Discussion

Although the consequences of forest disturbance on forest-associated wildlife have been intensively studied (Barlow et al., 2016; Meyer et al., 2016), previous studies have been predominantly observational and consequently limited in their capacity to disentangle spatial and temporal heterogeneity from disturbance effects (França et at., 2016). This limitation has led to recent calls for studies following the quasi-experimental framework of BACI designs (Bicknell et al., 2015; França et at., 2016). Here, we present evidence, by means of a BACI study, that relatively small man-made clearings had a weaker influence on the occupancy of Neotropical bats inhabiting the interiors and edges of forest fragments and matrix sites than temporal heterogeneity due to natural rates of occupancy turnover across the landscape. Additionally, we found a considerable increase in spatial turnover following fragment re-isolation, as evidenced by a decrease in assemblage similarity between CF and modified habitats (fragments, matrix). Sampling was conducted immediately after re-isolation and consequently we might have been unable to detect some effects that might take longer to manifest themselves (i.e. there could be time lags). Still, our results highlight that even small clearings pervasively impact bat assemblages in a regenerating fragmented landscape.

4.1. Species richness responses to fragment re-isolation

Our results revealed that for all habitats other than edges, species richness declined after fragment re-isolation. This decline was more pronounced for forest specialist than for generalist species. The magnitude of these declines in fragment interiors and the matrix was however similar to the decline observed in CF, our experimental controls. This

suggests that observed occupancy declines were unlikely the result of re-isolation, but rather reflect marked interannual variation in species occupancy or detectability.

Tropical assemblages exhibit profound spatiotemporal variation in response to resource availability (Haugaasen and Peres, 2007; Beja et al., 2010; Castro and Espinosa, 2015). Although seasonal differences in species richness, abundance and composition have been repeatedly documented across the tropics for many taxa, including bats at the BDFFP and elsewhere (Ramos Pereira et al., 2010; Cisneros et al., 2015; Ferreira et al., 2017), evidence for supra-annual fluctuations is scarce (Hodgkison et al., 2004; Kingston, 2013). Annual oscillations can however lead to misleading interpretations of ecological patterns, especially if data collection is conducted over small time windows (Meyer et al., 2016; Banks-Leite et al., 2012). By including experimental controls in our study design both before *and* after fragment re-isolation we were able to detect that even undisturbed sites underwent a significant decline in mean species occupancy, therefore precluding the possibly deceptive interpretation that the clearing of the 100 m strip of regrowth around the fragments had negatively impacted fragment and matrix species richness. Yet, some tropical vertebrates are known to make greater use of forest fragments during periods of low resource availability in order to expand their foraging areas or use them as stepping stones to disperse to areas of higher food availability (Maldonado-Coelho and Marini, 2004). Elevated use of secondary forest habitats, where fruit availability can be less seasonal, during periods of higher resource scarcity has also been reported for Neotropical frugivorous birds (Barlow et al., 2007). Consequently, under the absence of the experimental manipulation in forests fragments and surrounding matrix, a decrease in resource availability in CF could have led to displacement towards these habitats. However, since all sampled fragments were re-isolated we could not address this hypothesis.

Mounting evidence suggests that Neotropical bats respond, sometimes markedly, to habitat edges (Gorresen and Willig, 2004; Faria 2006; Meyer and Kalko, 2008; Klingbeil and Willig, 2009; Rocha et al., 2017). Following fragment re-isolation, edges were the only habitat not to experience a decline in species richness. In fact, even though statistical support was limited, we observed an increase in the mean number of both generalist and specialist species captured per survey visit after fragment re-isolation. Declines in species richness at edges have been suggested to be linked to the avoidance of these habitats by animalivorous bats which might relate to changes in the densities of preferred prey or to flight constraints imposed by increased vegetation clutter typical of forest edges (Meyer and Kalko, 2008; Rocha et al., 2017). This avoidance may be further accentuated by clutter constraints to echolocation due to the masking of echoes from prey by echoes reflecting from surrounding vegetation (Schnitzler and Kalko, 2001) and by reduced access to prey due to denser vegetation (Rainho et al., 2010). Vegetation-free forest streams and man-made tracks also appear to constitute important flyways for bats (Palmeirim and Etherdige, 1985; Adams et al., 2009; Webala et al., 2010; de Oliveira et al., 2015). The removal of the vegetation surrounding the fragments might therefore have freed bats from the restrictions imposed by a denser understory, reflected in the observed increase in species richness.

4.2. Species-specific responses

The assessment of the effects of forest disturbance on bat assemblages has been somewhat limited by the evaluation of pooled responses at the ensemble- or assemblage-levels through measures such as species richness, evenness or assemblage structure (e.g. Avila-Cabadilla et al., 2009; Mendenhall et al., 2014; Arroyo-Rodríguez et al., 2016; Rocha et

al., 2017). Due to the high species richness, such pooling of species may blur the detection of species-specific trends associated with the wealth of responses to environmental changes found in tropical communities, even among closely related species (Elmqvist et al., 2003). A major impediment to species-level assessments relates to the difficulty in obtaining information for rare species, which abound in tropical ecosystems and are often of greater conservation concern. Here, species-level assessments were achieved by means of a joint species distribution model framework which, by incorporating species-specific responses into a single hierarchical model, allowed the detection of the relationship between habitat covariables and species responses at both the species and community levels (Ovaskainen and Soinien, 2011; Ovaskainen et al., 2016a; b).

Strong statistical support for an increase in occupancy in the second sampling period (after fragment re-isolation) was only found for 7 of the 50 analysed species. Of these, *Artibeus obscurus* was the sole species for which there was strong statistical support for an increase in CF whereas all remaining species were found to increase either in edge or matrix sites. Interestingly, only one of the species (*Micronycteris sanborni*) for which strong statistical support for an increase in occupancy was observed is not a canopy frugivore (Bernard, 2001). Indeed, two species with canopy affinities (*Chiroderma trinitatum* and *C. villosum*) were only captured after fragment re-isolation and a third one, *Ametrida centurio*, was captured twice as often during the four visits to each of the edge and matrix sites after re-isolation than in the 8 visits preceding manipulation (Table S1). Canopy foraging bats have been suggested to make more use of open areas than species that forage in the understory (Kalko and Handley, 2001). This perception of increased use of open spaces by canopy species may however correspond to an artefact, relating to an anti-predator shift in the use of the vertical space in areas of reduced canopy cover. This "vegetation hugging" behaviour, in which prey species travel close to vegetation to avoid

the higher predation risk associated with crossing open spaces has been observed for several European vespertilionids (e.g. Schaub and Schnitzler, 2007) but had to date not been reported in the tropics or for frugivores (Lima and O'Keefe, 2013).

The most pronounced decline in occupancy following fragment re-isolation was found for *P. parnellii* in matrix habitats. The species is a high duty-cycle insectivorous bat with an echolocation characterized by long constant frequency signals, which allows for efficient prey detection in cluttered environments (Hiryu et al., 2016). Amazonian populations were found to present higher activity in habitats with more clutter, which also presented higher insect biomass (de Oliveira et al., 2015). By affecting vegetation density, the clearance of regrowth vegetation surrounding the fragments might have reduced matrix suitability for the species, leading to a pronounced decline in occupancy.

5. Conclusions

Our study presents experimental evidence that even relatively small clearings have pervasive impacts on species-rich Amazonian bat assemblages. However, these effects did not manifest as major changes in local diversity (measured as the mean number of species captured per survey visit) but mainly as changes in assemblage composition. These results align with the recent finding by Dornelas et al. (2014) that following anthropogenic modification many assemblages undergo biodiversity change, but not necessarily species loss. Our findings also align with results by Wilson et al. (2016) suggesting that assemblage composition may be a better predictor of how fragmentation affects biotic communities than species richness. Practitioners and researchers alike should therefore include metrics of assemblage composition when investigating temporal change across modified landscapes. Increased use of BACI approaches should also be

encouraged as it allows separating the confounding effects of natural temporal heterogeneity from disturbance responses.

The experimental clearings targeted by this study are somewhat more similar to large natural forest gaps (e.g. windthrows), in which tumbled trees lie scattered and rotting, encouraging quick secondary forest regrowth, than to anthropogenic clearings. Yet, in the Amazon, ranchers frequently clear secondary vegetation surrounding forest fragments to promote pasture areas for cattle (Laurance et al., 2007). The fragment re-isolation examined in this study somewhat mimics this re-opening of fragment edges by ranchers, offering important insights into the consequences of this common land-use practice. Additionally, the results presented here have important implications for linear forest clearings originating from infrastructures such as roads, railroads and powerlines which constitute nowadays omnipresent features of human-modified tropical landscapes.

Acknowledgments

We would like to thank the many volunteers and mateiros that helped us during fieldwork and José L.C. Camargo, Rosely Hipólito and Ary Jorge Ferreira for logistic support. Funding was provided by the Portuguese Foundation for Science and Technology to C.F.J.M. (PTDC/BIA-BIC/111184/2009), R.R. (SFRH/BD/80488/2011) and A.L.-B. (PD/BD/52597/2014). F.Z.F. and P.E.D.B. were supported by a CAPES fellowship. Additional funding was provided by a Bat Conservation International student research fellowship to R.R. OO was supported by the Academy of Finland (Grants no. 250444 and 273253) and the Research Council of Norway (CoE grant no. 223257). This research was conducted under ICMBio permit (26877-2) and constitutes the publication number XXX of the BDFFP technical series.

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Supplementary Material

Figure S1 - Picture of A) 1 ha (right) and 100 ha fragments (left); and B) 1 ha fragment after experimental isolation by clearing of the surrounding regrowth vegetation. Pictures by A.L.-B.

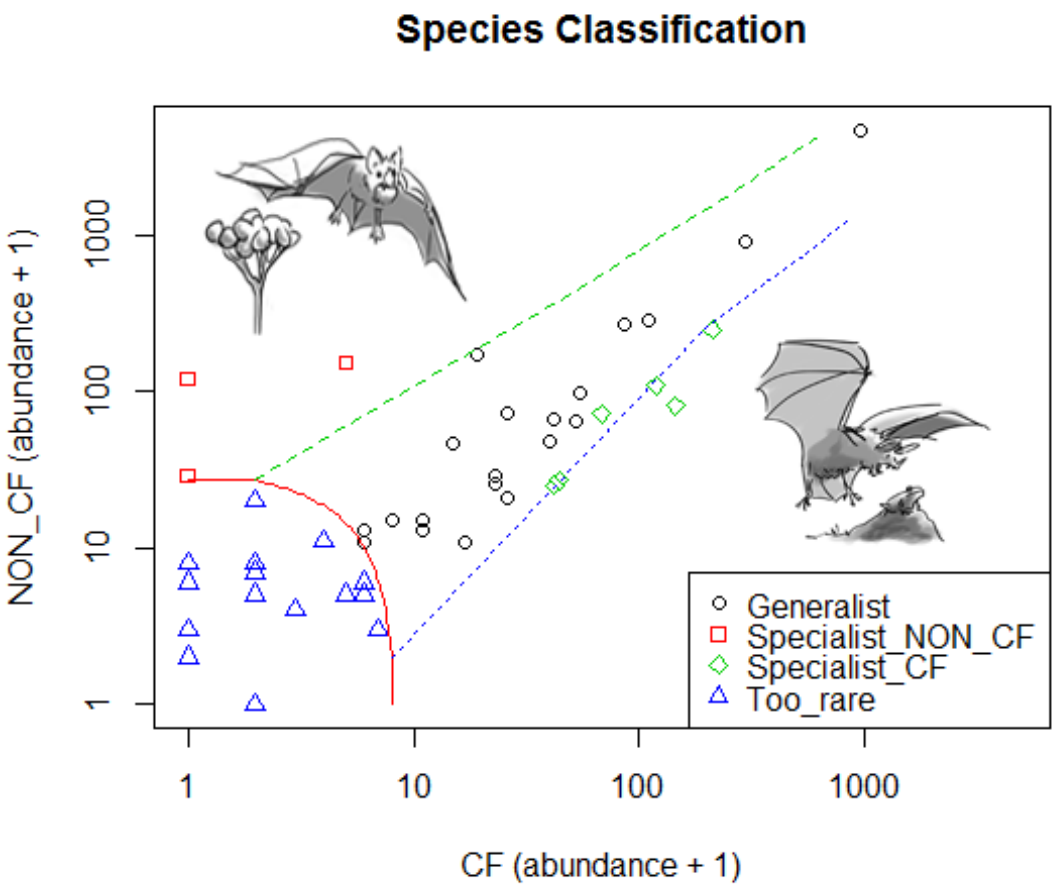

Figure S2 - Habitat affinity classification results based 10, 311 bat captures at continuous forest, forest fragments and secondary forest sites of the BDFFP between 1996 and 2014. Classification was based on the super-majority specialization threshold (*K* =2/3, *P* =0.001), with adjustment for multiple comparisons. Abbreviations: CF = Continuous forest; NON_CF = Non continuous forest (captures at fragments and secondary forest sites).

Table S1 – Number of captures for each phyllostomid bat species and *Pteronotus parnellii* sampled in at the Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil before and after fragment re-isolation. Abbreviations for habitat affinity: Gen – Generalis; Spe – Specialist.

Taxon	Species code	Habitat affinity	Before fragment re-isolation				After fragment re-isolation				Total
			Continuous forest	Fragment			Continuous forest	Fragment			
				Interior	Edge	Matrix		Interior	Edge	Matrix	
Phyllostomidae											
Anoura caudifer	Acau	Spe	1	1	1	1					4
Ametrida centurio	Acen	Spe			2	2			3	5	12
Artibeus cinereus	Acin	Gen	9	7	4	7	1	6	1	5	40
Artibeus concolor	Acon	Gen	3	8	9	28	2	7	13	14	84
Artibeus gnomus	Agon	Gen	6	5	5	10	2	4	2	4	38
Artibeus lituratus	Alit	Spe	10	5	1	15	4	3		1	39
Artibeus obscurus	Aobs	Gen	9	25	31	46	16	8	1	2	138
Artibeus planirostris	Apla	Gen	7	8		3					18
Carollia brevicauda	Cabre	Gen	11	28	16	28	7	6	14	8	118
Chrotopterus auritus	Caur	Spe	2	2			1				5
Carollia castanea	Ccas	Spe		2							2
Choeroniscus minor	Cmin	Spe	1	6					1		8
Carollia perspicillata	Cper	Gen	136	622	402	503	38	134	301	196	2332
Chiroderma trinitatum	Ctri	Spe							1	2	3
Chiroderma villosum	Cvil	Spe							1	1	2
Desmodus rotundus	Drot	Gen	3	2		1	1	1			8
Glyphonycteris daviesi	Gdav	Spe	1			2	1				4

Glossophaga soricina	Gsor	Gen	2	5	1						8
Glyphonycteris sylvestris	Gsyl	Spe	1								1
Lampronycteris brachyotis	Labra	Spe		1							1
Lichonycteris degener	Lich	Spe									0
Lophostoma carrikeri	Lcar	Spe		1	2	1		1	1		6
Lophostoma brasiliense	Lobra	Spe	1		4					2	7
Lophostoma schulzi	Lsch	Gen	3	2	1	1	1	2	1	2	13
Lophostoma silvicolum	Lsil	Spe	27	14	10	9	9	6	5	1	81
Lonchophylla thomasi	Ltho	Gen	8	16	3	1	11			2	41
Mimon crenulatum	Mcre	Gen	13	15	12	9	3	12	1	3	68
Micronycteris hirsuta	Mhir	Spe		1		1					2
Mesophylla macconnelli	Mmac	Spe	13	5	2	1	7	1	5	3	37
Micronycteris megalotis	Mmeg	Gen		1			1	1			3
Micronycteris microtis	Mmic	Gen	2	3	1	2			1		9
Micronycteris sanborni	Msan	Spe							2		2
Micronycteris schmidtorum	Msch	Spe		1							1
Phyllostomus discolor	Pdis	Gen		3		1					4
Phyllostomus elongatus	Pelo	Spe	12	7	2	1	4	1			27
Phyllostomus hastatus	Phas	Spe	1	1	1						3
Platyrrhinus helleri	Phel	Spe			2	1					3
Phylloderma stenops	Pste	Gen	2	3	2	2	2	4	1		16
Rhinophylla pumilio	Rpum	Gen	76	174	83	89	20	61	25	25	553
Sturnira lilium	Slil	Gen								1	1
Sturnira tildae	Stil	Gen		1	4	13			5	6	29
Trachops cirrhosus	Tcir	Spe	36	28	2	11	5	8	1	1	92
Trinycteris nicefori	Tnic	Gen	4	2	2	1				2	11

Tonatia saurophila	Tsau	Gen	19	25	4	2	3	6			59
Uroderma bilobatum	Ubil	Gen		1	2	2		3		2	10
Vampyressa pusilla	Vpus	Spe									0
Vampyriscus bidens	Vbid	Gen	6	5	1		6	3	1	1	23
Vampyrum spectrum	Vspe	Spe									0
Vampyriscus brocki	Vbro	Spe		2	1		1	1			5
Mormoopidae											
Pteronotus parnellii	Ppar	Spe	92	53	25	39	25	24	12	3	273
Total captures			**517**	**1091**	**638**	**833**	**171**	**303**	**399**	**292**	**4244**

Table S2 - Assemblage similarity between continuous forest and modified habitats (fragment interiors, fragment edges and fragment matrix), prior and following fragment re-isolation. We defined the similarity between two assemblages as the correlation between model predicted occurrence probabilities (log-transformed). The values in the table show posterior mean similarities between communities inhabiting continuous forests and modified habitats for the two study periods. Abbreviations as follows: CF = Continuous forest; FI = Fragment interiors; FE = Fragment edge; FM = Fragment matrix. Sampling period, before and after fragment re-isolation, is denoted as 1 (before) and 2 (after).

All species	CF1	CF2	FE1	FE2	FI1	FI2	FM1	FM2
CF1	1.00	0.80	0.66	0.43	0.82	0.75	0.68	0.41
CF2	0.80	1.00	0.56	0.35	0.69	0.70	0.56	0.41
FE1	0.66	0.56	1.00	0.62	0.71	0.69	0.77	0.62
FE2	0.43	0.35	0.62	1.00	0.47	0.52	0.62	0.64
FI1	0.82	0.69	0.71	0.47	1.00	0.74	0.71	0.44
FI2	0.75	0.70	0.69	0.52	0.74	1.00	0.71	0.54
FM1	0.68	0.56	0.77	0.62	0.71	0.71	1.00	0.62
FM2	0.41	0.41	0.62	0.64	0.44	0.54	0.62	1.00
Generalists	CF1	CF2	FE1	FE2	FI1	FI2	FM1	FM2
CF1	1.00	0.82	0.63	0.40	0.86	0.75	0.60	0.36
CF2	0.82	1.00	0.55	0.38	0.74	0.72	0.53	0.34
FE1	0.63	0.55	1.00	0.70	0.75	0.66	0.78	0.68
FE2	0.40	0.38	0.70	1.00	0.53	0.56	0.71	0.71
FI1	0.86	0.74	0.75	0.53	1.00	0.74	0.71	0.47
FI2	0.75	0.72	0.66	0.56	0.74	1.00	0.70	0.48
FM1	0.60	0.53	0.78	0.71	0.71	0.70	1.00	0.66
FM2	0.36	0.34	0.68	0.71	0.47	0.48	0.66	1.00
Specialists	CF1	CF2	FE1	FE2	FI1	FI2	FM1	FM2
CF1	1.00	0.77	0.63	0.40	0.79	0.71	0.66	0.33
CF2	0.77	1.00	0.49	0.28	0.61	0.64	0.51	0.33
FE1	0.63	0.49	1.00	0.54	0.63	0.63	0.72	0.51
FE2	0.40	0.28	0.54	1.00	0.38	0.46	0.56	0.59
FI1	0.79	0.61	0.63	0.38	1.00	0.66	0.64	0.25
FI2	0.71	0.64	0.63	0.46	0.66	1.00	0.64	0.43
FM1	0.66	0.51	0.72	0.56	0.64	0.64	1.00	0.49
FM2	0.33	0.33	0.51	0.59	0.25	0.43	0.49	1.00

Table S3 - Assemblage similarity between continuous forest and modified habitats (fragment interiors, fragment edges and matrix sites), before and after fragment re-isolation. We defined the similarity between two assemblages as the correlation between model-predicted occurrence probabilities (log-transformed). The values in the table show posterior mean similarities between assemblages in CF and modified habitats for the two study periods. Values are based on the amount of primary forest present within a 500 m buffer centred on each sampling site. Mean, low and high forest cover stand for predictions of assemblage similarity based on model-predicted occurrence probabilities for mean (33%), minimum (4%) and maximum (100%) values of primary forest cover within a 500 m radius.

	Fragment interior		**Fragment edge**		**Fragment**	
Mean forest cover	*Generalists*	*Specialists*	*Generalists*	*Specialists*	*Generalists*	*Specialists*
Before re-isolation	0.86	0.79	0.63	0.63	0.60	0.66
After re-isolation	0.72	0.64	0.38	0.28	0.34	0.33
% change[1]	15.97	18.82	39.72	54.57	43.68	50.39
Posterior probability[2]	0.87	0.86	0.94	**0.97**	0.93	**0.97**
Low forest cover						
Before re-isolation	0.79	0.72	0.58	0.58	0.57	0.64
After re-isolation	0.66	0.59	0.34	0.25	0.31	0.3
% change[1]	16.01	17.73	41.58	42.20	45.78	53.29
Posterior probability[2]	0.8	0.78	0.92	**0.97**	0.91	**0.97**
High forest cover						
Before re-isolation	0.92	0.86	0.71	0.69	0.65	0.7
After re-isolation	0.77	0.68	0.45	0.34	0.38	0.37
% change[1]	15.91	21.11	36.96	51.25	40.93	47.14
Posterior probability[2]	**0.96**	0.92	**0.95**	**0.98**	0.93	**0.97**

[1] Percent change in assemblage similarity before and after fragment re-isolation.

[2] Posterior probability of assemblage similarity being higher before than after fragment re-isolation; values showing high statistical support (posterior probability > 95%) are highlighted in bold.

CHAPTER 5

Neotropical bats in a recovering fragmented landscape: effects of secondary forest regrowth on specialist and generalist species

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CHAPTER 5

Neotropical bats in a recovering fragmented landscape: effects of secondary forest regrowth on specialist and generalist species.

Abstract

Tropical deforestation continues apace and rates of forest loss and fragmentation are projected to increase in coming decades. Understanding how matrix dynamics, especially secondary forest regrowth, can ameliorate fragmentation impacts is key to understanding species persistence in human-modified tropical landscapes. We surveyed bat assemblages in continuous forest, forest fragments and secondary forest matrix habitats, ~15 and ~30 years after forest clearance at the Biological Dynamics of Forest Fragments Project, a whole-ecosystem fragmentation experiment in the Central Brazilian Amazon. Species were classified according to their habitat affinity into old-growth specialists and habitat generalists and, for both groups, we used a joint species distribution modeling framework to investigate temporal changes in species occupancy and abundance across the landscape. We observed that the regeneration of the second growth matrix between ~1996 and ~2011 had overall positive effects on the occupancy and abundance of specialist bats across all sampled habitats. Conversely, effects on generalist species were negligible for forest fragments and negative for secondary forest. Species responses were idiosyncratic and although specialist species benefited from forest regeneration, evidence was limited for increasing assemblage similarity between continuous and modified habitats (fragments and secondary forest) with regeneration time. This suggests that forest succession leads to improved, yet modified, assemblages. Our results, although contingent on the existence of nearby source populations, highlight the conservation

relevance of secondary forests for reverting faunal declines in humanized tropical landscapes and offer a much needed sign of hope amidst gloomy forecasts for tropical biodiversity**.**

Keywords: Amazon, bats, habitat fragmentation, habitat restoration, hierarchical Bayesian models, forest succession, second growth, specialization.

Introduction

Humanity's global footprint is so ubiquitous and far-reaching that many argue that we now live in a new geological epoch, the Anthropocene (Waters et al., 2016). Habitat loss and fragmentation are pervasive and conspicuous features of this new historical context, which, in combination with other human-related threats, are compelling the planet into a "sixth wave of extinction" (Dirzo et al., 2014; Ceballos et al., 2015).

The scars of the Anthropocene defaunation are being carved deep into the planet's biodiversity strongholds, the tropical forests (Malhi et al., 2014). As large swaths of old-growth forest give way to expanding humanized landscapes, species persisting in forest remnants are left to endure the pervasive consequences of increased isolation and decreased area (Haddad et al., 2015). Landscape-wide assemblage dynamics in fragments created in the aftermath of deforestation are dependent, to a large extent, on the nature of the matrix within which forest patches are embedded (Watling et al., 2011). Conservation science has traditionally conceived the modified matrix as a "sea" of hostile habitat, in which fragments act as "islands" and this analogy has guided much of the theory and practice of the field (Watling et al., 2011; He & Hubbell, 2011). However, equating forest fragments with island ecosystems, while appropriate in some situations, fails to

accommodate the heterogeneous and dynamic nature of most present-day modified landscapes (Driscoll et al., 2013; Mendenhall et al., 2014).

Vertebrate assemblage dynamics in tropical land-bridge islands have painted a dire portrait of the consequences of forest fragmentation in true island systems (Meyer & Kalko, 2008; Gibson et al., 2013; Benchimol & Peres, 2015). Mainland studies that also construed fragments as true islands, have arrived at similar pessimistic narratives (Ferraz et al., 2003; Wearn et al., 2013). However, direct comparisons between these two systems (true islands *vs* mainland) have revealed that assemblages persisting in forest patches embedded in terrestrial human-dominated landscapes defy the patterns exhibited by their water-embedded analogues (Mendenhall et al., 2014; Wolfe et al., 2015).

Second growth nowadays constitutes the predominant type of forest cover across the tropics (Chazdon, 2014), providing myriad services and natural products to human populations worldwide, and key habitat for countless forest-dwelling species (Barlow et al., 2007; Chazdon, 2008; Gardner et al., 2009). Although some fragmentation-related extinctions can be averted by forest regeneration (Stouffer et al., 2011; Wearn et al., 2013; Wolfe et al., 2015), the role of second growth in biodiversity conservation remains controversial (Melo et al., 2013; Sloan et al., 2015; Arroyo-Rodríguez et al., 2015). Central to the debate is the capacity of secondary forest to accommodate old-growth specialist species and to buffer the impacts of fragmentation on assemblages living in forest remnants (Barlow et al., 2007; Gibson et al., 2011; Chazdon, 2014).

We surveyed bats, a taxon demonstrably sensitive to habitat modification (Meyer et al., 2016) in six experimental forest fragments (3 of 1 ha and 3 of 10 ha) and seven secondary forest sites, ~15 and ~30 years after forest clearance in the early 1980s at the Biological Dynamics of Forest Fragments Project (BDFFP) (Fig. 1; see Methods), the world's largest

and longest-running fragmentation experiment, located in the central Brazilian Amazon (Laurance et al., 2011). Determining the responses of tropical species to habitat change is often hindered by the rarity of old-growth specialists for which data are often too sparse for reliable inference at the species level. This commonly leads to the exclusion of less captured species (which are often of conservation concern) from the analysis or to several species to be jointly analysed according to particular groups (e.g. feeding guilds), thus preventing the detection of species-specific responses. Here, we overcome this difficulty by employing a joint species distribution modelling framework, that combines species-specific models into a single hierarchical model that allows the detection of the relationship between environmental variables and species responses simultaneously at the species and community levels (Ovaskainen et al., 2016a).

Our overarching aim was to examine the effect of matrix regeneration on old-growth specialist and habitat generalist species across the three main habitats of the BDFFP: continuous primary forest, primary forest fragments and secondary forest matrix. Specifically, we predicted that the maturation of the secondary forest surrounding forest fragments between study periods would provide extra resources for old-growth specialists, leading to increases in occupancy and abundance in this group both within fragments and the secondary regrowth matrix. Conversely, we expected that the successional advance of the secondary vegetation would have diminished the availability of food resources for bats specialised on early-successional plants, hence reducing the abundance of generalists in the same habitats. Additionally, since similarity in structure and floristic composition between secondary and primary forests increases with regeneration time (DeWalt et al., 2003; Chazdon, 2014) we anticipated bat assemblage similarity between continuous forest and secondary forest to be higher ~30 years after forest clearance (~1996) than half-way through the study period (~15 years after forest

clearance; ~2011). Similarly, during the same period, the reduction in fragment-matrix contrast was expected to increase the assemblage similarity between forest fragments and continuous forest.

Methods

Study area. Bat surveys took place at the Biological Dynamics of Forest Fragments Project (BDFFP), approximately 80 km north of Manaus (2°30'S, 60°W, 30-125 m above sea level), state of Amazonas, Brazil (Fig. 1). Forest in the ~1,000 km^2 study area is non-flooded (*terra firme*) rainforest with a canopy height of 30-37 m and emergent trees reaching 55 m (Mesquita et al., 1999). The BDFFP is among the most biodiverse in the world (tree species richness often exceeding 280 species ha^{-1}; Oliveira & Mori, 1999) and, with the exception of the experimental fragmentation, has been sheltered from anthropogenic disturbances such as logging and fires. The climate is characterized by a dry season between June and October and annual rainfall varies from 1,900 to 3,500 mm. Fragments were isolated from continuous forest by distances of 80-650 m in the early 1980s and are categorized into size classes of 1, 10 and 100 ha. Fragments were originally located within cattle ranches (3,000-5,000 ha each) but poor soils and low productivity dictated the abandonment of livestock activities and fragments became gradually surrounded by secondary forest dominated mainly by *Vismia* spp. and *Cecropia* spp. (Mesquita et al., 2015). Following secondary forest proliferation, fragment isolation was maintained by clearing a 100 m-wide strip of regrowth at intervals of ~10 years around most experimental forest fragments. During this study fragment re-isolation occurred between 1999 and 2001. For a description of the study landscape experimental manipulation and ecosystem-wide responses see Laurance et al. (2011).

Bat sampling. In both study periods (1996-2002 and 2011-2013) we sampled bats in forest fragments (six sites, three of 1 ha and three of 10 ha), secondary forest (seven sites) and continuous forest (six sites) (Fig. 1). Sampling started at dusk and nets were deployed until 0:00 am, being revised at intervals of ~20 minutes. Bias in capture rates due to net shyness was avoided by spacing visits to the same site by periods of three to four weeks and sampling was interrupted during heavy rains.

During the first sampling period bats were surveyed from January 1996 to June 1999 in forest fragments and continuous forest sites by E. Sampaio, and from October 2001 to November 2002 in secondary forest by P. Bobrowiec. The mist-netting protocol consisted of eight (secondary forest sites) and 18 to 24 (fragments and continuous forest sites) ground-level mist nets (12 m x 2.5 m) placed along existing trails. We surveyed fragment and continuous forest sites on seven to 12 nights and secondary forest sites between three to seven nights. Total mist net effort was 8757, 9429 and 860 mist-net hours (mnh; 1 mnh equals one 12-m net open for 1 h) for continuous forest, fragments and secondary forests, respectively. Captured bats were identified and had standard morphometric and demographic data collected. For this first study period, detailed site descriptions, methods and results for fragments and continuous forest can be found in Sampaio (2001) and Sampaio et al. (2003) and for secondary forest in Bobrowiec & Gribel (2010). Our analyses are restricted to ground-level captures in fragment and continuous forest interiors (Sampaio et al., 2003) and to captures in *Vismia*- and *Cecropia*-dominated secondary forest (Bobrowiec & Gribel, 2010).

During the second period we re-surveyed all 19 sites between August 2011 and June 2013. The mist-netting protocol consisted of seven (secondary forest sites) and 14 (fragments and continuous forest sites) ground-level mist nets (12 x 2.5 m) placed at existing trails. Total mist net effort was 4009, 3963 and 1941 mnh for continuous forest, fragments and

secondary forests, respectively. Similarly to the first period captured bats were identified and had standard morphometric and demographic data collected.

We restricted our analysis to phyllostomid bats and *Pteronotus parnelli* since all other captured species are inadequately sampled with ground-level mist-nets. Taxonomy follows Gardner (2007).

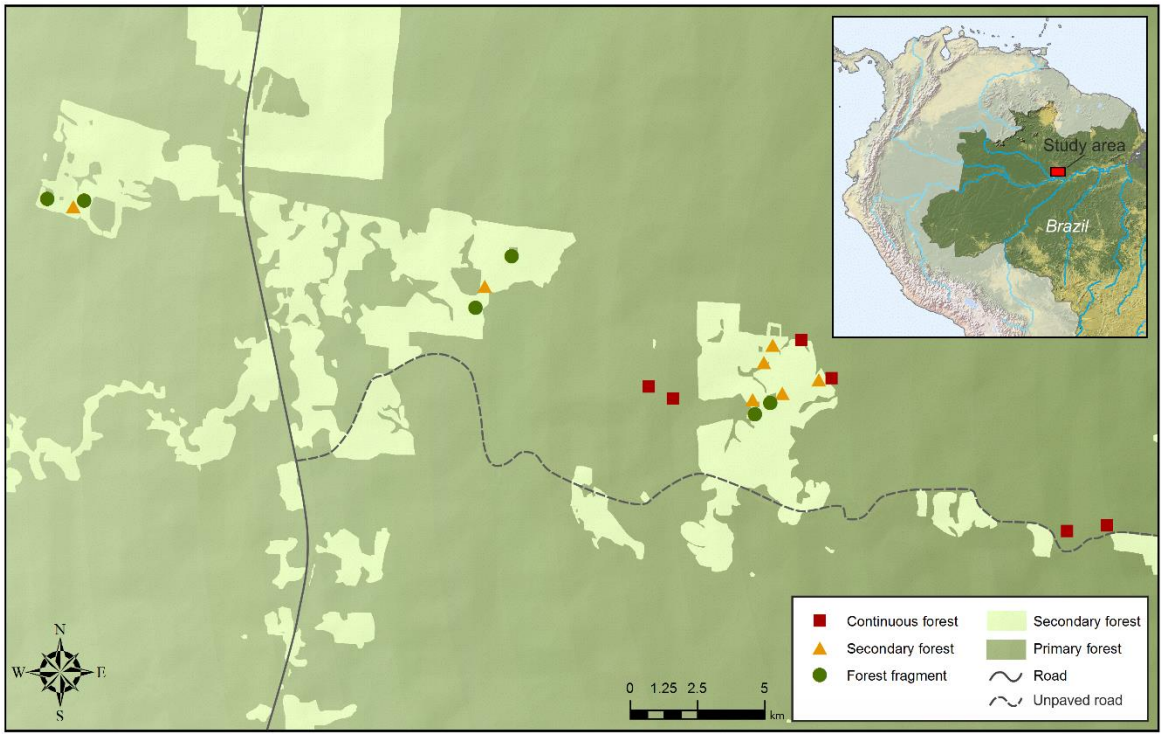

Figure 1. The Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil. Light green represents secondary forest matrix and dark green continuous forest and forest fragments. Location of the study area within Brazil is shown in the map inset.

Species affinities to primary and secondary forest. We used the statistical approach developed by Chazdon et al. (2011) to classify species into one of four groups: primary forest specialists, secondary forest specialists, generalists or too rare to classify. Classification was based on the whole dataset of 10,311 captures of 50 species sampled at the BDFFP between 1996 and 2014. Only a sub-set of these captures (6,109) was subsequently used in the joint species distribution models (see below). The method uses a multinominal model based on species relative abundance in both habitats (here defined as continuous primary forest *vs* forest fragments and secondary forest) and simultaneously minimizes bias due to different sampling effort between habitats and due to insufficient captures of rare species. Classification was conducted in R v.3.0.2 (R Development Core Team 2013) using the vegan package and setting a significance level of $P = 0.01$. We conservatively grouped primary forest specialists and species too rare to classify into a single group and since only two species were assigned to the secondary forest category, they were lumped together with generalists. We therefore considered two functional groups in our analysis: primary forest species and species too rare to classify (hereafter "specialist species") and generalists and secondary forest specialists (hereafter "generalist species").

Joint species distribution model. We applied a hierarchical joint species distribution model (Ovaskainen & Soininen, 2011; Warton et al., 2015; Ovaskainen et al., 2016a, b) to relate the bat occurrence data to environmental covariates. As a sampling unit, we considered one mist-netting session in one site (n = 301 mist-netting sessions). As the data involved a large fraction of zeros (70%), we applied a hurdle model, thus modeling separately presence-absence (model 1), and abundance conditional on presence (model 2). In model 1, the response variable was the vector of presence-absences of all the 50

species, and we assumed a Bernoulli distribution with a probit link-function. In model 2, the response variable was the vector of abundances of those species which were present, whereas species that were absent were considered as missing data. In this case, we assumed an overdispersed Poisson distribution with a log-link function. Abundance was measured as the number of captured individuals, of which we subtracted one to match the range of the assumed distribution (overdispersed Poisson) with the range of the response variable (note that conditional on presence, the smallest value for number of individuals is one, not zero). As explanatory variables, we included habitat type (categorical: continuous forest, fragment, or secondary forest), survey period (first (1996-2002) or second survey (2011-13)), percentage of secondary forest cover within a radius of 500 m from each site and the log-transformed survey effort, measured as mist-net hours (1 mist-net hour [mnh] equals one 12-m net open for 1 h). We also included an interaction between survey period and habitat type, as well as an interaction between survey period and secondary forest cover. Percent secondary forest cover was measured from a detailed digital map of the BDFFP landscape based on Landsat Thematic Mapper data from 1996 (for the first survey period) and from 2011 (for the second survey period) – see Carreiras et al. (2014) for image classification details. A buffer size of 500 m was selected so to avoid overlap between neighboring sites.

To account for repeated measurements at the same sites, we assumed a site-level random effect, implemented at the community level using the latent factor approach of Ovaskainen et al. (2016a). As species traits, we included the classification into habitat generalists and specialists. To account for phylogenetic non-independence, we followed Abrego et al. (2017) to structure the error variance with a phylogenetic correlation matrix, derived from a phylogenetic tree under the diffusion model. The phylogenetic tree was

taken from Jones et al. (2002). We fitted the model in the Bayesian framework using the Gibbs sampler of Ovaskainen et al. (2016a, b).

We used the parameterized model to predict the expected species richness and number of captured individuals (for all species and separately for generalists and specialists) in each habitat class and study period per survey visit. Species richness was computed as the sum (over the species) of the occurrence probabilities predicted by model 1. Number of individuals was computed as the sum (over the species) of species-specific abundances, computed as the product of occurrence probability (from model 1) and abundance conditional on presence (prediction of model 2 plus one). In these predictions, we standardized the mist netting effort to the mean value of a given habitat category across both study periods, and the percentage of secondary forest to the mean value of a particular habitat type during a given survey period. We calculated the difference to measure the change in expected species richness and number of captured individuals in each habitat type between the two survey periods. Species-level responses were assessed by computing the difference between the occurrence probability and mean number of individuals expected to be captured per survey visit between the first and the second period.

Turnover metrics are considered better suited to quantify biodiversity change in local assemblages through time than simple temporal trends of within-sample diversity (temporal α diversity) (Dornelas et al., 2014). To characterize assemblage turnover, we computed assemblage similarity between the different habitat categories as well as between the two study periods. Assemblage similarity was defined as the correlation between model-predicted occurrence probabilities or abundances (both log-transformed) (Ovaskainen & Soininen, 2011). We performed these calculations for all species, and separately for generalists and specialists only.

Results

We captured 4,028 bats in the first period (35, 33 and 22 species in continuous forest, forest fragments and secondary forest respectively; 20 species shared between the three habitats) and 2,081 bats in the second period (33, 34 and 35 species in continuous forest, forest fragments and secondary forest respectively; 26 species shared between the three habitats). Twenty-seven species were classified as primary forest specialists whereas 23 were classified as habitat generalists (Table S1).

Our modelling results revealed that the regeneration of the BDFFP matrix between the two periods had overall positive effects on the estimated occupancy and abundance of specialist bats in secondary forest sites and fragments, whereas effects on generalist species were negligible (fragments) or negative (secondary forest) (Fig. 2). Model predictions indicate that for old-growth specialist bats the mean number of species expected to be captured during a survey visit nearly doubled in fragments (0.81 in ~1996; 1.5 in ~2011) while remaining virtually unchanged for generalist species (3.63 in ~1996; 4.17 in ~2011). In secondary forest, this figure also increased for specialist bats (0.62 in ~1996; 0.91 in ~2011), while decreasing for generalist species (4.5 in ~1996; 2.81 in ~2011) and in continuous forest increased for both groups (1.81 in ~1996; 2.79 in ~2011 (specialists) and 3.47 in ~1996; 4.7 in ~2011 (generalists)) (Fig. 2). The mean number of individuals captured during a given survey varied little between the first and second period in continuous forest and fragments but decreased by nearly 2/3 in secondary forest (from 23.24 in ~1996 to 8.39 in ~2011) (Fig. S1). In this habitat, generalists and specialists exhibited opposite trends between periods, with the mean number of individuals of generalist species declining from 22.55 in ~1996 to 7.3 in ~2011 and the mean number of individuals of specialist species increasing from 0.68 to 1.1 in the same period (Fig. 2).

Between ~1996 and ~2011 only 3 and 4 of the 27 species classified as specialists decreased in occupancy respectively in fragments and secondary forest. Furthermore, statistical support for these declines was limited (Fig. 3; Table S2). During the same period, out of the 27 specialists, the abundance increased for 25 in fragments and for 23 in secondary forest. In contrast, of the 23 species classified as generalists, 7 declined in occupancy in fragments and 17 in secondary forest (high statistical support for 1 and 7 species, respectively) (Fig. 3; Table S2). Seven generalist species declined abundance in fragments and 17 in secondary forest (Fig. 3).

Assemblage similarity between continuous forest and fragments increased slightly with time for generalists when considering both occupancy and abundance but declined for specialists. In secondary forests, occupancy and abundance based assemblage similarities declined for both groups. However, statistical support for these trends was limited (Table 1; See Table S3 for assemblage similarity comparisons for all species combined).

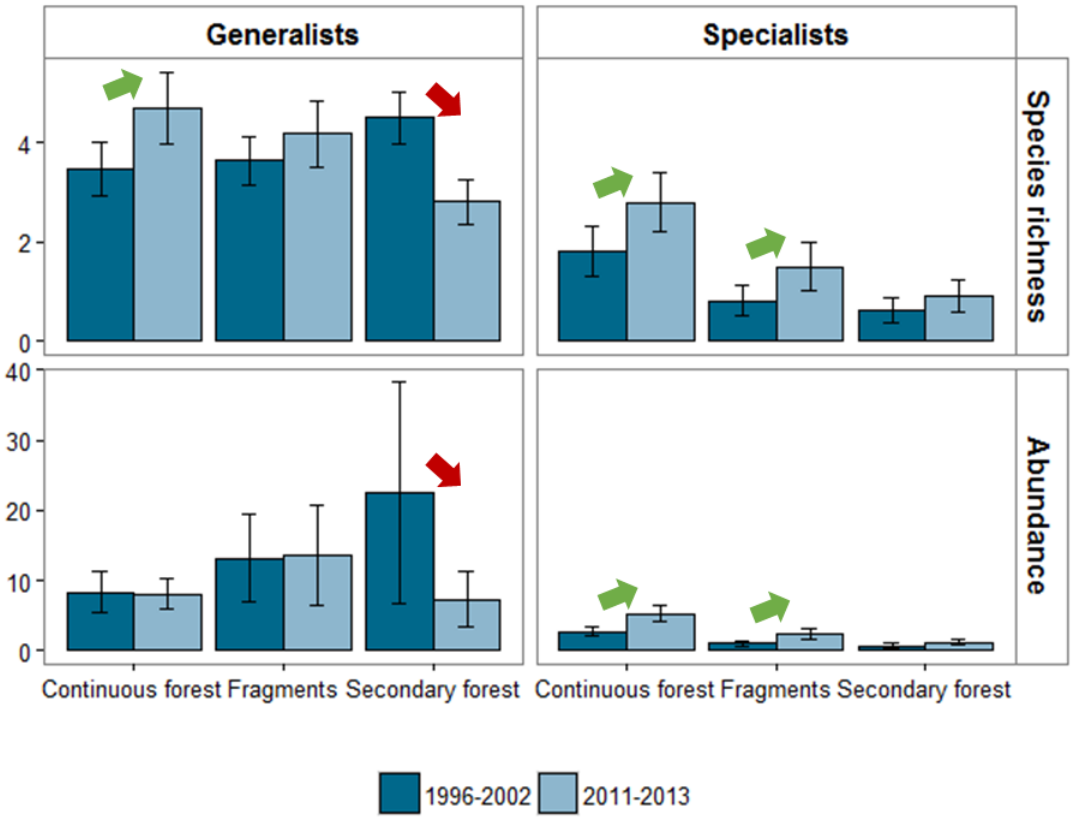

Figure 2. Bat species richness and abundance of generalist and specialist bats in continuous forest, fragments and secondary forest, ~15 years and ~30 years after experimental forest clearance. Plotted are the predictions of the mean number of species and the mean number of individuals (± posterior standard deviation) captured per survey visit. Capture effort was standardized within each habitat category and thus the results are comparable only between periods but not across habitat types. Arrows stand for high statistical support (posterior probability > 95%) for the predictions being higher (upward-pointing) or lower (downward-pointing) ~30 years after experimental forest clearance (2011-2013) than ~15 years after experimental forest clearance (1996-2002). Species' habitat affinities are reported in Table S1 (for classification description see Methods) and results for all species combined are provided in Fig. S1.

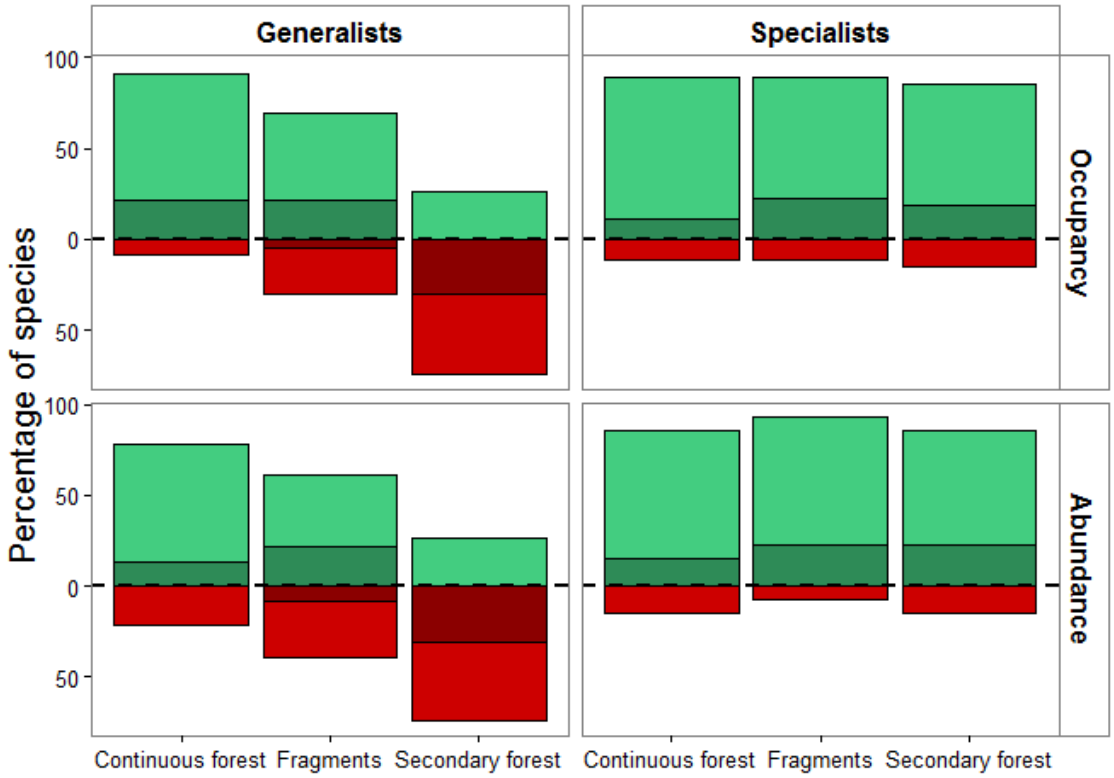

Figure 3. Change in species occupancy probability and abundance of generalist and specialist bats in continuous forest, fragments and secondary forest, ~15 years and ~30 years after experimental forest clearance. Plotted is the percentage of species with positive (green) and negative (red) changes in probability of occurrence and mean number of individuals predicted to be captured per survey visit between the first and second period (~15 and ~30 after experimental forest clearance). Dark and light colours represent respectively, percentage of species with high (posterior probability > 95%) and low statistical support (posterior probability < 95%). Predictions account for within-habitat differences in capture effort between the two periods. Species-specific values are reported in Table S2; species' habitat affinities are given in Table S1 (for classification description see Methods).

Table 1. Assemblage similarity between continuous forest and modified habitats (fragments and secondary forest), ~15 years and ~30 years after experimental forest clearance. We defined the similarity between two assemblages as the correlation between model-predicted occurrence probabilities or abundances (both log-transformed). The values in the table show posterior mean similarities between assemblages inhabiting continuous forests and modified habitats for the two study periods, as well as the posterior probability by which the similarities were lower in the first period than in the second.

	Fragments		**Secondary Forest**	
Generalists	*Occupancy*	*Abundance*	*Occupancy*	*Abundance*
1996-2002	0.64	0.71	0.60	0.68
2011-2013	0.76	0.79	0.51	0.56
Posterior probability	0.8	0.74	0.21	0.31
Specialists				
1996-2002	0.84	0.85	0.78	0.78
2011-2013	0.74	0.76	0.61	0.63
Posterior probability	0.16	0.16	0.09	0.09

Discussion

Contrary to catastrophic faunal declines observed in rodent communities by Gibson et al. (2013) in the forest islands of the Chiew Larn reservoir in Thailand we found that, during a similar time window (~20 years, Gibson et al., 2013; ~15 years, our study), most species of the mega-diverse bat assemblage at the BDFFP increased their occupancy and abundance across a second growth-dominated landscape. This recovery was mostly due to the recolonization of previously deforested areas and forest fragments by specialist species, which increased in all sampled habitats during the second period. Notwithstanding major morphological and ecological differences between rodents and bats, the widely different trajectories exhibited by assemblages inhabiting true island

systems and fragments embedded within a regenerating matrix reinforce the potential of second growth forests to mitigate fragmentation-related extinctions.

As hypothesized, we found that the maturation of second growth surrounding the BDFFP fragments lead to a landscape-wide increase in the occupancy and abundance of specialists, while reducing the occupancy and abundance of generalists in secondary forest sites. Our results therefore mirror the recovery documented for beetle (Quintero & Roslin, 2005) and bird (Stouffer et al., 2011) assemblages following the development of secondary vegetation in the matrix between forest fragments at the BDFFP. However, it is worth emphasizing that the BDFFP is surrounded by vast expanses of continuous forest harbouring healthy source populations and is buffered from selective logging, fires, species invasions, and many other ancillary threats plaguing contemporary tropical fragmented landscapes (Laurance et al., 2011). The recovery here documented is therefore likely to represent a best-case scenario and patterns reported might be harder to observe under conditions that increasingly characterize the majority of human-modified tropical landscapes.

Our results have important implications for the interpretation of land-use change studies using space-for-time approaches. Researchers rarely have the opportunity to collect data prior to the main disturbance events that mould humanized landscapes. Consequently, studies often have to rely on nearby sites where the target impact has not yet taken place and assume that these accurately mimic pre-disturbance conditions (França et al., 2016). Here, we show that the species richness of generalists and both the species richness and abundance of specialists have increased in our reference sites in continuous forest, indicating considerable temporal heterogeneity in undisturbed forest assemblages over a period of ~15 years. This suggests that space-for-time results may be undermined not only by confounding effects arising from spatial heterogeneity but also by constraints

associated with the temporal heterogeneity of the assemblages inhabiting sites used as spatial surrogates. This shifting baseline somewhat limits our capacity to attribute the observed changes in fragment and secondary forest bat assemblages entirely to the effect of matrix maturation. However, the contrasting temporal trends in the species richness of generalists in continuous forest and secondary forest i.e. increase in continuous forest *vs.* decrease in secondary forest, indicates that secondary forest regeneration plays an important role in the assemblage dynamics across the landscape. Yet, the lack of understanding of the extent of spatial and temporal dynamics of generalist and specialist species in continuous forest and how these fluctuations may relate to patterns in fragmented landscapes still blurs our understanding of these systems and therefore should be a high priority for future research.

Despite the controlled, experimental conditions of the BDFFP, our findings add to an increasing body of evidence (e.g. Mendenhall et al., 2014; Wolfe et al., 2015) emphasizing that the transposition of patterns of biodiversity persistence in island ecosystems to fragmented terrestrial settings can be hampered by the dynamic nature of human-dominated landscapes, and consequently predictions under the island biogeographic framework can distort our understanding and misguide conservation strategies. Accordingly, and in light of the contrasting temporal trajectories of specialist and generalist species at the BDFFP, alternative theoretical frameworks, importantly, countryside biogeography (Pereira & Daily, 2006; Mendenhall et al., 2013), in which species' differential habitat affinities can be accommodated, emerge as better suited for forecasting biological changes in human-made habitats (Mendenhall et al., 2014).

In spite of some noteworthy regional declines in deforestation rates (e.g. Brazilian rainforests), tropical forest loss has increased by more than 2000 km^2/year since the beginning of the millennium (Hansen et al., 2013). Much of these deforested areas will

be used to meet the growing demands for food and biofuel of an increasing human population (Laurance et al., 2014). However, following forest clearing, some converted areas are allowed to regenerate, giving birth to human-modified landscapes in which secondary forests account for an increasing proportion of total forest cover (Chazdon 2014). Our results, although contingent on the existence of nearby source populations, add to the evidence that secondary forests offer a tremendous opportunity for both assisted and non-assisted habitat restoration (Chazdon, 2008; Chazdon & Guariguata, 2016). Among bats, frugivorous species are effective seed dispersers, especially of pioneer plant species (de la Peña-Domene et al., 2014) and gleaning insectivores play essential roles in the reduction of herbivory levels through trophic control of herbivorous arthropods (Kalka et al., 2008; Maas et al., 2015). Populations able to persist in primary forest remnants can therefore enhance second growth successional processes and by doing so, aid in maintaining the provision of ecosystem services and improve habitat quality and connectivity in regenerating tropical forests.

Laurance et al. (2007) observed that despite the carefully controlled experimental conditions of the BDFFP and the broadly similar biotic and abiotic conditions of the project's study area prior to the initial forest manipulation, tree communities in different areas of the landscape have diverged with time leading to the suggestion of the landscape divergence hypothesis. In spite of the signs of recovery exhibited by specialist species across our study landscape ~30 years after forest clearance, our results do not support an increase in assemblage similarity between continuous forest and secondary forest over time, therefore matching the expectation of increased divergence with time suggested by the landscape divergence hypothesis. This, together with evidence that bat assemblages in smaller fragments (≤ 10 ha) and secondary forest sites still differ considerably from continuous forest in terms of species richness, evenness, composition and abundance

(Rocha et al., 2016), suggest that the second growth matrix at the BDFFP still acts as an environmental filter. This filtering shapes bat assemblages in a trait-mediated manner, selectively benefiting bat species with a phytophagous diet and reduced body mass (Farneda et al., 2015). Similar pervasive consequences of forest clearance can still be detected in birds (Mokross et al., 2014; Figueira et al., 2015) and primates (Lenz et al., 2014) in the BDFFP landscape, highlighting that, although second growth can be of conservation significance, primary forest is of irreplaceable value (Barlow et al., 2007; Gibson et al., 2011).

To a large extent, the conservation potential of the world's tropical secondary rainforests depends on the legal framework underpinning their governance. In the Brazilian Amazon, the state of Pará has recently introduced legislation recommending protection of >20-year-old secondary forest (as identified through inspection of satellite images) as well as younger stands depending on the total stand basal area of native trees and palms (Vieira et al., 2014). Although legal protection *per se* does not ensure long-term safeguarding of the services provided by second-growth forests, it represents a critical step towards their management. We therefore urge researchers, practitioners and policy makers to adopt similar protective measures, especially in areas where primary forest is scarce or highly fragmented.

Human-modified tropical landscapes are in continuous flux, with areas of secondary forest being converted to agricultural land and vice-versa. Vegetation disturbances, both anthropogenic and natural (e.g. fire), are irregular in space and time, moulding mosaic landscapes in which the classic split between fragments and matrix is blurred (del Castillo, 2015). The ability of species to persist in such dynamic landscapes will ultimately depend on the interaction between their intrinsic traits (e.g. mobility and life span), interspecific interactions and the availability of habitat capable of meeting their

specific resource needs. Although hotly debated (Wright & Muller-Landau, 2006a,b; Gardner et al., 2007; Laurance, 2007; Gibson et al., 2011), the "rescue" potential of secondary forests in these dynamic landscapes is far from negligible (Dunn, 2004; Chazdon et al., 2009; Dent & Wright, 2009; Chazdon, 2014). While adding to mounting evidence that secondary forests are of conservation value, our, and many other long-term studies at the BDFFP (reviewed by Laurance et al., 2016) and elsewhere in the tropics (e.g. Barlow et al., 2007; Martin et al., 2013) reveal that continuous primary forest and large (> 100 ha) forest fragments are of overwhelming importance for the conservation of tropical biodiversity.

Acknowledgments

We would like to thank the multitude of volunteers and field assistants who helped collecting the data, the BDFFP management team for logistic support and João M.B. Carreiras for providing secondary forest layers for our study area. Funding was provided by the Portuguese Foundation for Science and Technology to C.F.J.M. (PTDC/BIA-BIC/111184/2009), R.R. (SFRH/BD/80488/2011) and A.L.-B. (PD/BD/52597/2014). P.E.D.B. was supported by a CAPES fellowship. OO was supported by the Academy of Finland (Grants no. 250444 and 273253) and the Research Council of Norway (CoE grant no. 223257). This research was conducted under ICMBio permit (26877-2) and is publication number XXX in the BDFFP technical series.

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Supplementary Material

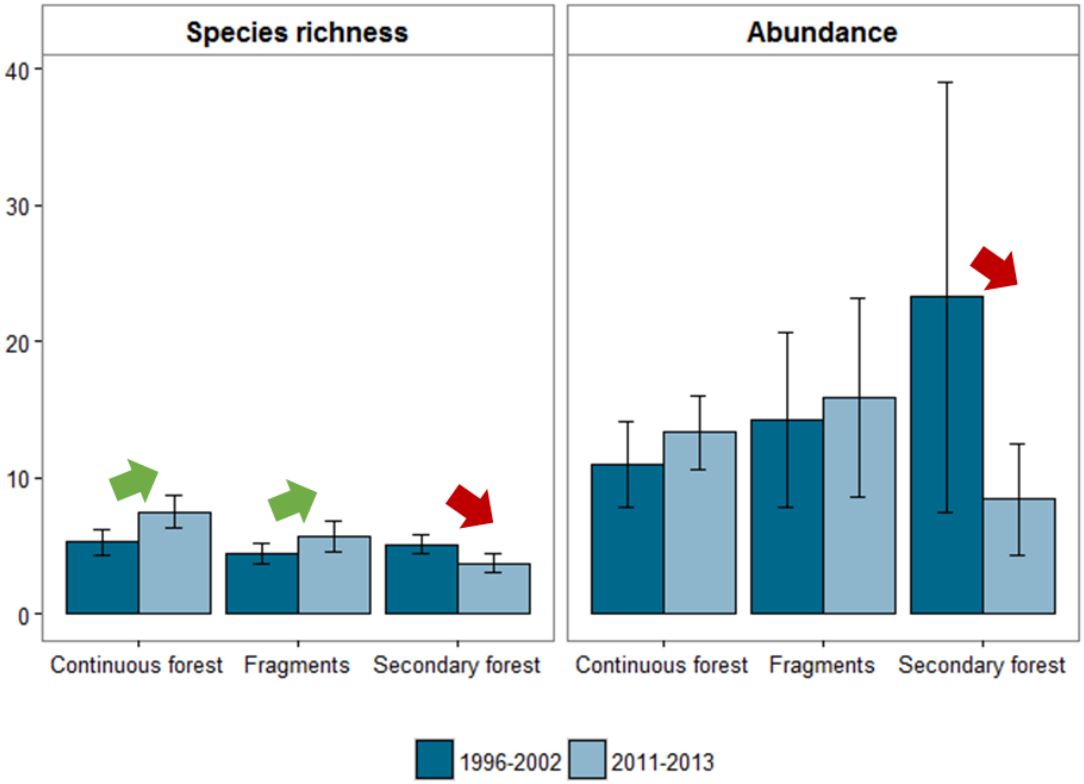

Figure S1. Bat species richness and abundance in continuous forest, fragments and secondary forest, ~15 years and ~30 years after experimental forest clearance. Plotted are the predictions of the mean number of species and the mean number of captured individuals (± posterior standard deviation) of all species combined per survey visit. Capture effort was standardized within each habitat category and thus the results are comparable only between periods but not across habitat types. Arrows stand for high statistical support (posterior probability > 95%) for the predictions of the posterior probabilities being higher (upward-pointing) or lower (downward-pointing) ~30 years after experimental forest clearance than in 1996-2002. Species' habitat affinities are reported in Table S1 (for classification description see Methods).

Table S1. Bat species sampled at the Biological Dynamics of Forest Fragments Project, Central Amazon, Brazil, ~15 years (1996-2002) and ~30 years (2011-2013) after forest clearing. Habitat abbreviations: CF = Continuous forest; F = Fragments; SF = Secondary forest.

Species	Habitat affinity	1996-2002			2011-2013			Total
		CF	F	SF	CF	F	SF	
Artibeus cinereus	Generalist	11	24	2	8	6	4	55
Artibeus concolor	Generalist	12	17	22	3	4	18	76
Artibeus gnomus	Generalist	2	3	2	8	2	6	23
Artibeus obscurus	Generalist	70	148	10	14	18	7	267
Artibeus planirostris	Generalist	31	51	1	7	5	3	98
Carollia brevicauda	Generalist	59	57	31	13	25	31	216
Carollia perspicillata	Generalist	607	1076	618	181	530	353	3365
Desmodus rotundus	Generalist	14	18	1	7	1	1	42
Glossophaga soricina	Generalist	3		4	2	2		11
Lonchophylla thomasi	Generalist	15	20		7	15	3	60
Lophostoma schulzi	Generalist	11			2	1	1	15
Micronycteris megalotis	Generalist	8	7	3	1	1	1	21
Micronycteris microtis	Generalist				4	2	3	9
Mimon crenulatum	Generalist	29	12	2	15	9	5	72
Phylloderma stenops	Generalist	13	10	1	6	3	2	35
Phyllostomus discolor	Generalist	4	7		2	2		15
Rhinophylla pumilio	Generalist	160	211	81	74	131	83	740
Sturnira lilium	Generalist		14	2			1	17
Sturnira tildae	Generalist	3	21	12	1	1	9	47
Tonatia saurophila	Generalist	16	12	5	26	12	5	76
Trinycteris nicefori	Generalist	6	1		3	2	4	16
Uroderma bilobatum	Generalist		8			1	2	11
Vampyriscus bidens	Generalist	9	1		5	4	5	24
Ametrida centurio	Specialist	1					2	3
Anoura caudifer	Specialist				1			1
Artibeus lituratus	Specialist	39	23	4	16	2	8	92
Carollia castanea	Specialist					3	2	5
Chiroderma trinitatum	Specialist	5	1					6
Chiroderma villosum	Specialist							0
Choeroniscus minor	Specialist	2	3		1	5		11
Chrotopterus auritus	Specialist	1	2		2	1	1	7
Glyphonycteris daviesi	Specialist				1		2	3

Glyphonycteris sylvestris	Specialist	5	2		1			8
Lampronycteris brachyotis	Specialist					1	1	2
Lichonycteris degener	Specialist	1						1
Lophostoma brasiliense	Specialist						1	1
Lophostoma carrikeri	Specialist					1	1	2
Lophostoma silvicolum	Specialist	57	44	2	40	11	12	166
Mesophylla macconnelli	Specialist	20	4	1	10	2	2	39
Micronycteris hirsuta	Specialist	2	1					3
Micronycteris sanborni	Specialist							0
Micronycteris schmidtorum	Specialist							0
Phyllostomus elongatus	Specialist	17	3	5	14	5	3	47
Phyllostomus hastatus	Specialist	3	1		1			5
Platyrrhinus helleri	Specialist		1				1	2
Pteronotus parnellii	Specialist	68	27	5	74	24	29	227
Trachops cirrhosus	Specialist	68	10	1	52	26	7	164
Vampyressa pusilla	Specialist							0
Vampyriscus brocki	Specialist					2		2
Vampyrum spectrum	Specialist	1						1
Total		**1373**	**1840**	**815**	**602**	**860**	**619**	**6109**

Table S2. Species-specific predictions for occupancy probability and abundance in continuous forest, fragments and secondary forest, ~15 years and ~30 years after experimental forest clearance. Predictions account for within-habitat differences in capture effort between the two periods. Posterior probability stands for the probability of the predictions for occupancy and abundance being higher in 1996-2002 than in 2011-2013; values showing high statistical support (posterior probability > 95%) are highlighted in bold.

	Occupancy			**Abundance**		
Species	**1996-2002**	**2011-2013**	**Posterior probability**	**1996-2002**	**2011-2013**	**Posterior probability**
Continuous Forest						
Ametrida centurio	0.007	0.008	0.423	0.008	0.009	0.426
Anoura caudifer	0.004	0.015	0.814	0.005	0.015	0.814
Artibeus cinereus	0.080	0.191	**0.966**	0.099	0.209	0.946
Artibeus concolor	0.099	0.119	0.594	0.138	0.130	0.434
Artibeus gnomus	0.034	0.154	**0.994**	0.038	0.164	**0.989**
Artibeus lituratus	0.197	0.226	0.634	0.428	0.381	0.377
Artibeus obscurus	0.311	0.348	0.651	0.487	0.409	0.283
Artibeus planirostris	0.193	0.193	0.497	0.251	0.221	0.403
Carollia brevicauda	0.427	0.345	0.206	0.645	0.428	0.066
Carollia castanea	0.006	0.006	0.406	0.007	0.007	0.400
Carollia perspicillata	0.814	0.897	0.849	4.014	2.806	0.114
Chiroderma trinitatum	0.019	0.014	0.291	0.021	0.015	0.300
Chiroderma villosum	0.002	0.002	0.383	0.002	0.002	0.377
Choeroniscus minor	0.023	0.044	0.709	0.023	0.045	0.720

Chrotopterus auritus	0.021	0.045	0.840	0.022	0.052	0.851
Desmodus rotundus	0.097	0.241	**0.960**	0.114	0.267	**0.951**
Glossophaga soricina	0.032	0.052	0.689	0.034	0.055	0.689
Glyphonycteris daviesi	0.006	0.019	0.811	0.006	0.020	0.811
Glyphonycteris sylvestris	0.031	0.046	0.623	0.032	0.047	0.623
Lampronycteris brachyotis	0.003	0.006	0.666	0.003	0.006	0.660
Lichonycteris degener	0.006	0.008	0.506	0.006	0.008	0.503
Lonchophylla thomasi	0.099	0.169	0.823	0.115	0.197	0.829
Lophostoma brasiliense	0.005	0.012	0.720	0.005	0.015	0.743
Lophostoma carrikeri	0.005	0.014	0.763	0.006	0.016	0.789
Lophostoma schulzi	0.057	0.094	0.791	0.064	0.107	0.797
Lophostoma silvicolum	0.300	0.522	**0.980**	0.414	0.927	**0.997**
Mesophylla macconnelli	0.116	0.140	0.617	0.142	0.166	0.589
Micronycteris hirsuta	0.012	0.012	0.414	0.013	0.012	0.406
Micronycteris megalotis	0.067	0.072	0.500	0.069	0.073	0.503
Micronycteris microtis	0.011	0.051	**0.951**	0.012	0.053	0.949
Micronycteris sanborni	0.001	0.003	0.526	0.001	0.003	0.517
Micronycteris schmidtorum	0.001	0.002	0.523	0.001	0.002	0.523
Mimon crenulatum	0.158	0.242	0.826	0.216	0.375	0.891
Phylloderma stenops	0.088	0.112	0.631	0.103	0.154	0.717
Phyllostomus discolor	0.021	0.064	0.929	0.025	0.072	0.914
Phyllostomus elongatus	0.116	0.264	**0.980**	0.135	0.296	**0.966**
Phyllostomus hastatus	0.026	0.044	0.723	0.027	0.046	0.723
Platyrrhinus helleri	0.003	0.004	0.483	0.003	0.005	0.477

Pteronotus parnellii	0.532	0.642	0.791	0.834	1.756	**0.994**
Rhinophylla pumilio	0.633	0.752	0.889	1.567	1.569	0.523
Sturnira lilium	0.005	0.006	0.437	0.006	0.006	0.434
Sturnira tildae	0.030	0.047	0.683	0.042	0.057	0.603
Tonatia saurophila	0.111	0.337	**0.997**	0.138	0.481	**1.000**
Trachops cirrhosus	0.360	0.672	**1.000**	0.522	1.382	**1.000**
Trinycteris nicefori	0.049	0.097	0.806	0.050	0.098	0.800
Uroderma bilobatum	0.005	0.008	0.586	0.006	0.009	0.551
Vampyressa pusilla	0.002	0.002	0.543	0.002	0.003	0.531
Vampyriscus bidens	0.004	0.008	0.677	0.004	0.008	0.674
Vampyriscus brocki	0.044	0.108	0.940	0.054	0.116	0.891
Vampyrum spectrum	0.006	0.011	0.626	0.007	0.012	0.629
Fragments						
Ametrida centurio	0.004	0.010	0.689	0.004	0.011	0.686
Anoura caudifer	0.001	0.008	0.811	0.001	0.009	0.817
Artibeus cinereus	0.139	0.144	0.489	0.190	0.161	0.346
Artibeus concolor	0.139	0.119	0.374	0.201	0.138	0.237
Artibeus gnomus	0.024	0.067	0.883	0.029	0.071	0.866
Artibeus lituratus	0.134	0.059	0.089	0.237	0.086	0.069
Artibeus obscurus	0.328	0.261	0.243	0.676	0.343	**0.029**
Artibeus planirostris	0.191	0.150	0.323	0.311	0.173	0.134
Carollia brevicauda	0.377	0.383	0.517	0.632	0.728	0.677
Carollia castanea	0.005	0.045	**0.951**	0.006	0.068	**0.969**
Carollia perspicillata	0.928	0.955	0.700	8.250	7.816	0.377

Chiroderma trinitatum	0.008	0.009	0.466	0.009	0.009	0.460
Chiroderma villosum	0.001	0.002	0.597	0.001	0.002	0.597
Choeroniscus minor	0.024	0.097	0.940	0.025	0.103	0.943
Chrotopterus auritus	0.009	0.026	0.800	0.010	0.030	0.823
Desmodus rotundus	0.099	0.077	0.357	0.123	0.087	0.300
Glossophaga soricina	0.009	0.048	0.931	0.010	0.052	0.937
Glyphonycteris daviesi	0.002	0.008	0.794	0.002	0.008	0.794
Glyphonycteris sylvestris	0.013	0.012	0.400	0.013	0.013	0.417
Lampronycteris brachyotis	0.001	0.016	**0.963**	0.001	0.017	**0.966**
Lichonycteris degener	0.003	0.010	0.743	0.003	0.012	0.757
Lonchophylla thomasi	0.149	0.223	0.809	0.170	0.353	0.920
Lophostoma brasiliense	0.001	0.008	0.903	0.001	0.009	0.911
Lophostoma carrikeri	0.002	0.018	**0.969**	0.002	0.020	**0.974**
Lophostoma schulzi	0.008	0.049	0.949	0.010	0.053	0.937
Lophostoma silvicolum	0.245	0.259	0.540	0.301	0.349	0.617
Mesophylla macconnelli	0.034	0.053	0.726	0.037	0.059	0.717
Micronycteris hirsuta	0.004	0.007	0.560	0.005	0.008	0.580
Micronycteris megalotis	0.054	0.053	0.480	0.055	0.055	0.477
Micronycteris microtis	0.006	0.049	**0.969**	0.006	0.053	**0.971**
Micronycteris sanborni	0.000	0.003	0.729	0.000	0.003	0.734
Micronycteris schmidtorum	0.000	0.002	0.734	0.000	0.002	0.740
Mimon crenulatum	0.051	0.154	**0.986**	0.069	0.201	**0.977**
Phylloderma stenops	0.070	0.088	0.606	0.077	0.114	0.657
Phyllostomus discolor	0.037	0.053	0.611	0.042	0.070	0.657

Phyllostomus elongatus	0.033	0.107	**0.960**	0.035	0.126	**0.969**
Phyllostomus hastatus	0.007	0.012	0.631	0.007	0.014	0.646
Platyrrhinus helleri	0.007	0.009	0.497	0.008	0.010	0.489
Pteronotus parnellii	0.202	0.316	0.840	0.266	0.558	0.931
Rhinophylla pumilio	0.706	0.836	0.926	1.886	2.567	0.926
Sturnira lilium	0.074	0.014	**0.029**	0.091	0.015	**0.017**
Sturnira tildae	0.107	0.050	0.109	0.182	0.063	0.054
Tonatia saurophila	0.078	0.207	**0.994**	0.092	0.265	**0.994**
Trachops cirrhosus	0.067	0.372	**1.000**	0.081	0.714	**1.000**
Trinycteris nicefori	0.011	0.064	**0.963**	0.011	0.066	**0.963**
Uroderma bilobatum	0.035	0.039	0.517	0.045	0.044	0.460
Vampyressa pusilla	0.001	0.003	0.794	0.001	0.003	0.794
Vampyriscus bidens	0.001	0.022	**0.991**	0.001	0.024	**0.989**
Vampyriscus brocki	0.014	0.091	**0.980**	0.017	0.107	**0.977**
Vampyrum spectrum	0.001	0.006	0.803	0.001	0.006	0.806
Secondary forest						
Ametrida centurio	0.004	0.026	0.940	0.004	0.027	0.946
Anoura caudifer	0.002	0.002	0.671	0.002	0.002	0.677
Artibeus cinereus	0.114	0.058	0.166	0.131	0.068	0.189
Artibeus concolor	0.359	0.100	**0.003**	0.639	0.245	**0.040**
Artibeus gnomus	0.076	0.083	0.554	0.081	0.091	0.563
Artibeus lituratus	0.138	0.049	0.080	0.151	0.069	0.131
Artibeus obscurus	0.350	0.109	**0.003**	0.376	0.118	**0.003**
Artibeus planirostris	0.086	0.038	0.174	0.088	0.039	0.180

Carollia brevicauda	0.650	0.312	**0.000**	1.192	0.492	**0.003**
Carollia castanea	0.006	0.039	0.946	0.007	0.044	0.949
Carollia perspicillata	0.988	0.877	**0.003**	16.277	4.338	**0.000**
Chiroderma trinitatum	0.003	0.005	0.754	0.003	0.005	0.757
Chiroderma villosum	0.000	0.002	0.900	0.000	0.002	0.906
Choeroniscus minor	0.007	0.006	0.523	0.007	0.006	0.520
Chrotopterus auritus	0.004	0.014	0.883	0.004	0.014	0.886
Desmodus rotundus	0.054	0.018	0.200	0.056	0.018	0.197
Glossophaga soricina	0.138	0.012	**0.000**	0.139	0.012	**0.000**
Glyphonycteris daviesi	0.001	0.019	**0.971**	0.001	0.020	**0.971**
Glyphonycteris sylvestris	0.003	0.008	0.800	0.003	0.008	0.803
Lampronycteris brachyotis	0.001	0.013	**0.989**	0.001	0.013	**0.989**
Lichonycteris degener	0.001	0.002	0.814	0.001	0.002	0.814
Lonchophylla thomasi	0.029	0.028	0.583	0.033	0.032	0.597
Lophostoma brasiliense	0.001	0.009	**0.969**	0.001	0.010	**0.969**
Lophostoma carrikeri	0.001	0.012	**0.989**	0.001	0.012	**0.989**
Lophostoma schulzi	0.012	0.017	0.711	0.013	0.018	0.709
Lophostoma silvicolum	0.104	0.147	0.726	0.110	0.160	0.734
Mesophylla macconnelli	0.028	0.039	0.694	0.028	0.042	0.714
Micronycteris hirsuta	0.001	0.004	0.806	0.001	0.004	0.803
Micronycteris megalotis	0.091	0.023	0.066	0.095	0.023	0.054
Micronycteris microtis	0.011	0.037	0.903	0.012	0.039	0.900
Micronycteris sanborni	0.000	0.002	0.889	0.000	0.002	0.889
Micronycteris schmidtorum	0.000	0.001	0.931	0.000	0.001	0.931

Mimon crenulatum	0.084	0.061	0.331	0.095	0.069	0.343
Phylloderma stenops	0.045	0.022	0.251	0.050	0.025	0.257
Phyllostomus discolor	0.015	0.008	0.383	0.023	0.010	0.363
Phyllostomus elongatus	0.074	0.034	0.177	0.090	0.040	0.174
Phyllostomus hastatus	0.004	0.003	0.580	0.004	0.003	0.580
Platyrrhinus helleri	0.002	0.010	0.949	0.002	0.011	**0.951**
Pteronotus parnellii	0.169	0.351	**0.954**	0.193	0.473	**0.974**
Rhinophylla pumilio	0.896	0.692	**0.014**	2.621	1.285	**0.000**
Sturnira lilium	0.080	0.020	0.094	0.085	0.022	0.091
Sturnira tildae	0.245	0.069	**0.014**	0.349	0.100	**0.020**
Tonatia saurophila	0.134	0.091	0.263	0.151	0.101	0.254
Trachops cirrhosus	0.064	0.101	0.783	0.070	0.112	0.780
Trinycteris nicefori	0.014	0.057	0.929	0.015	0.058	0.920
Uroderma bilobatum	0.008	0.026	0.863	0.009	0.029	0.869
Vampyressa pusilla	0.000	0.003	0.946	0.000	0.003	0.949
Vampyriscus bidens	0.001	0.008	0.949	0.001	0.008	0.949
Vampyriscus brocki	0.021	0.058	0.880	0.022	0.066	0.889
Vampyrum spectrum	0.000	0.003	0.906	0.000	0.003	0.906

Table S3. Assemblage similarity between continuous forest and modified habitats (fragments and secondary forest), ~15 years and ~30 years after experimental forest clearance. Values correspond to the between-habitat correlation of the model's predictions of occurrence probabilities and abundance (log-transformed), computed for those two environments. Posterior probabilities stand for the probability of the assemblage similarity between continuous forest and the modified habitat (fragments or secondary forest) being lower in first than in the second period.

	Fragments		**Secondary Forest**	
	Occupancy	*Abundance*	*Occupancy*	*Abundance*
1996-2002	0.833	0.846	0.788	0.8
2011-2013	0.795	0.807	0.67	0.678
Posterior probability	0.309	0.329	0.08	0.09

CHAPTER 6

General discussion

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General Discussion

Unearthing the capacity of fragmented tropical landscapes to retain biodiversity is one of the key research topics in conservation science. However, despite intense research efforts, the vast majority of studies on the subject have been based on short-term projects. Consequently, time-related complexities associated with fragmentation resulting from time-lags, system history and temporal variation in resource quantity and quality remain poorly understood. The primary objective of this dissertation was to analyse some of the factors that affect the spatial and both short- and long-term temporal responses of tropical vertebrates to fragmentation, using bats as model taxa. The previous chapters addressed specific questions about the spatial (chapter 2 and 3) and temporal (chapter 4 and 5) variation of bat assemblages across the experimentally fragmented landscape of the BDFFP and detailed their conclusions and conservation implications. Here, I integrate the key findings and relate them to the current ecological and conservation literature. I additionally discuss some of the study limitations, outline some of the major conservation implications and suggest avenues for future research.

Bat responses to spatial heterogeneity in fragmented forest landscapes

Fragmentation is a landscape-level phenomenon and plentiful evidence supports that the magnitude of the ecological impacts of deforestation are affected by the size and spatial arrangement of the remaining forest patches as well as the type of matrix in which they are embedded (Ewers and Didham 2006; Watling et al. 2011). Bats are no exception to this and, similarly to other taxa, are affected by landscape-scale composition and

configuration (Trevelin et al. 2013; Ripperger et al. 2015). Accumulating evidence now supports that tropical bats present complex species- and ensemble-specific responses that are dependent on spatial scale (reviewed in Meyer et al. 2016). Landscape-scale disturbances (e.g. area reduction, isolation and edge effects) interact with within-forest disturbances such as changes in forest structure due, for instance, to the increase of pioneer trees near habitat edges or the loss of large canopy and emergent trees (Laurance et al. 2000; Laurance et al. 2006; Faria et al. 2009). The consequences of local- (see e.g. Marciente et al. 2015 and de Oliveira et al. 2015) and landscape-scale disturbances (see e.g. Cisneros et al. 2014; Arroyo-Rodríguez et al. 2016 and Chambers et al. 2016) on tropical bats have, however, overwhelmingly been studied in isolation (but see Meyer and Kalko 2008). Recent evidence shows that the consideration of both patch-scale and landscape-scale disturbance variables can lead to dramatically different perceptions regarding the impact of forest modification (Barlow et al. 2016). Consequently, previous studies analysing separately the within-patch and landscape-level disturbances for tropical bats, while providing important insights regarding bat responses to modified landscapes, may have delivered an incomplete understanding of population-, ensemble- and assemblage-level changes due to the interacting effects of local- and landscape-scale drivers. This thesis has expanded previous studies by examining the combined effects of metrics of local-scale habitat quality and landscape context on assemblage- and ensemble-level responses to fragmentation in Neotropical bats (chapter 2) and by considering gender–specific differences in the response to these metrics (chapter 3). The depth of these analyses was further expanded by the explicit consideration of biodiversity metrics at continuous forest, fragment interiors, forest edges and matrix habitats, thus allowing the investigation of how bats are affected by the full disturbance gradient in fragmented landscapes.

Many species are dependent on areas of primary forest and accordingly the loss of native vegetation has been linked to decreases in species diversity and changes in species composition (Fischer and Lindenmayer 2007). Several theoretical frameworks, the most well-known being the island biogeography (MacArthur and Wilson 1967) and metapopulation theories (Hanski 1998), have described the link between remaining native habitat and the species retained in modified landscapes. Despite considerable conceptual differences, these theories state that other things being equal, smaller fragments support fewer native species than larger fragments. Plentiful empirical evidence (including several studies at the BDFFP e.g. Ferraz et al. 2007 and Boyle and Smith 2010) now supports such species-area relationships. Our results, by showing that smaller ($\leq$ 10 ha) fragments present higher differences in species richness, evenness and assemblage composition relative to continuous forest than the 100 ha fragments, show that such area-effects on the magnitude of the fragmentation responses are noticeable on the bat assemblages of the BDFFP. This, despite the relatively low structural contrast between primary forest and the secondary forests that composes the regenerating matrix of our study landscape and the relatively high mobility of bats when compared with other non-flying vertebrates.

A patch-model underpins the assumptions that support the theoretical framework of the island biogeography and metapopulation theories (Fahrig and Merriam 1994). This model views patches as areas that provide habitat for species that are unable to live in the matrix of distinct vegetation in which the patches are embedded (Driscoll et al. 2013). Yet, while a clear distinction between patch and matrix habitats is sometimes reasonable, especially in high-contrast systems (e.g. land-bridge islands), in humanized landscapes, gradients of matrix quality mean that the characteristics that determine the availability of resources, influence dispersal and affect abiotic edge effects, change across space (and time). This,

in turn, influences the occurrence and abundance of species, consequently affecting the spatial dynamics of fragmented landscapes (Kupfer et al. 2006; Didham et al. 2012). The overwhelming importance of the matrix, which in some instances surpasses the importance of the size and spatial arrangement of fragments (Prugh et al. 2008), in mediating species-area relationships has been formally accommodated by countryside biogeography (Pereira and Daily 2006; Mendenhall et al. 2013). This theory, by acknowledging the differential affinities of species towards native and modified habitats, accounts for the fact that landscape-wide assemblage dynamics in fragmented landscapes are dependent to a large extent on the matrix in which native vegetation patches are embedded (Watling et al. 2011). We observed that assemblage- and ensemble-level responses (chapter 2) as well as sex-specific responses (chapter 3) to the different habitat classes were a likely reflection of the interaction between ensemble, species and sex-specific requirements and differential resource availability between the considered habitat classes (continuous forest, fragments, edges and matrix). For instance, and aligning with numerous previous studies (e.g. Gorresen and Willig 2004; Meyer and Kalko, 2008), we found that gleaning animalivorous bats at the BDFFP were particularly sensitive to fragmentation, exhibiting pronounced declines in abundance in fragments whereas frugivores, and in particular shrub frugivores such as *C. perspicillata* and *R. pumilio*, increased in abundance in fragment, edge and matrix habitats. Additionally, whereas the fewer captures of gleaning animalivores in modified habitats likely reflect a decline in the availability of roosts and food resources (Gorresen and Willig 2004; Meyer and Kalko 2008), the higher capture rate of frugivores seems to be attributable to the additional food resources provided by the *Vismia*- and *Cecropia*-dominated secondary vegetation (Bernard 2002; Horsley et al. 2015). The differential capacity of the matrix to accentuate or buffer the fragmentation effects on particular groups (e.g. ensembles, species or sexes)

emphasizes the importance of expanding traditional fragmentation studies, which are often limited to contrasting communities in the interior of fragments with control sites in undisturbed forest, to consider the full fragmentation gradient, i.e. to include edge and matrix habitats. This shift from patch-centered fragmentation studies towards a broader landscape-scale approach not only acknowledges the existence of gradients of habitat with differential capacity of accommodating species' needs but is also better suited to test conceptual frameworks that account for the influence of the matrix, such as countryside biogeography. Within the bat literature, a growing number of studies have adopted a matrix-inclusive approach (e.g. Rodríguez-San Pedro and Simonetti 2015; Arroyo-Rodríguez et al. 2016), however, the overall the number of studies explicitly considering the effects of landscape-scale composition and configuration is still small (Meyer et al 2016).

Bat responses to temporal heterogeneity in fragmented forest landscapes

There is a reduced number of studies that directly investigate temporal trends in fragmented landscapes and even fewer that evaluate how matrix use changes through time (but see Youngentob et al. 2013 and Haddad et al. 2015). Consequently, in contrast to the evaluation of spatial features, which has received some attention in the bat conservation literature, temporal variation, and in particular how bat responses to fragmentation are shaped by changes in matrix condition, remains little explored (Meyer et al. 2016).

It has long been acknowledged that species responses to fragmentation are sometimes delayed by considerable time lags (Ewers and Didham 2006) and it is widely accepted that the consideration of temporal variation and temporal scale is key for the understanding of fragment-matrix dynamics (Driscoll et al. 2013). However, although

several studies have addressed temporal questions under a space-for-time framework (e.g. Castro-Luna et al. 2007; Bobrowiec and Gibrel 2010), to date, long-term studies investigating the effects of fragmentation on tropical bats are limited to a set of related projects undertaken in a land-bridge island system in French Guiana (Cosson et al. 1999; Pons and Cosson 2002; Henry et al. 2010). By documenting bat assemblages both before, and several years after flooding, these studies provide compelling evidence for the occurrence of time lags over a period of ~10 years. However, although providing valuable insights into the temporal dynamics of fragmentation effects on tropical bats, the high-contrast water matrix in this system fails to adequately capture the dynamic nature and associated temporal heterogeneity of most human-modified tropical landscapes. In unflooded fragmented systems, the matrix often includes agricultural land and secondary vegetation, offering resources which patch-dependent species might use as food subsidy. Consequently, biodiversity responses in these systems may sharply contrast with those in fragmented landscapes with a static matrix (e.g. Mendenhall et al. 2014; Wolfe 2015).

The BDFFP has made substantial contributions to the study of temporal dynamics in responses of tropical taxa to forest modification (Laurance et al. 2011). Since the abandonment of livestock activities (late 80s), the pastures have gradually turned into secondary forests and the regrowth has lessened the effects of fragmentation on a wide array of taxa, including understory birds (Stouffer et al. 2011), dung beetles (Quintero and Roslin 2005) and primates (Boyle and Smith 2010). Unfortunately, the non-inclusion of bats amongst the first focal taxa of the project prevented the unveiling of the immediate impacts of the initial forest clearing on this group. However, one of the most important contributions of the BDFFP for the understanding of the effects of forest fragmentation immediately following the creation of the fragments is associated with a phenomenon known as the “sample effect” (Wilcox and Murphy 1985). This relates to the fact that due

to their rarity and patchy distributions, many tropical species may be absent from forest remnants solely due to not being present in the area at the time of fragment isolation. Ferraz et al. (2007) suggested that these sample effects may explain the absence of several rare understory birds in the fragments and since many of the region's bat species are naturally rare and patchily distributed (Meyer et al. 2015), it can be speculated that several bat species were likely absent from the fragments for the same reasons.

Chapter 4 tried to unveil the short-term consequences of fragment re-isolation on the bat assemblages now inhabiting the BDFFP fragments, however, the clearance of 100 m of secondary forests cannot be compared with the initial disturbance tied to the deforestation of large expanses of primary forest and consequently our results cannot be used to infer about the initial consequences of fragment isolation. Nonetheless, by demonstrating the existence of high natural spatiotemporal variability in the regions' bat assemblages our results suggest that sample effects might have affected the initial patterns of bat occupancy across the fragments. These sample effects associated with species' high spatiotemporal variability are likely to be commonplace across the tropics, where rare species with restricted distributions abound and consequently fragments (or, by analogy, protected areas) will have to be large enough for these species to be represented (Laurance et al. 2002).

Although the results from chapter 4 cannot inform about the initial consequences of fragment isolation, they reveal that dramatic changes in the structure of the matrix adjoining forest fragments can lead to pronounced and idiosyncratic responses in terms of species occupancy. This was particularly noticeable for primary forest specialists and at habitat edges. Whereas at fragment interiors and matrix habitats we observed a decrease in the mean number of species captured per survey visit following fragment re-isolation, at fragment edges it increased. This shows that communities can exhibit contrasting

temporal patterns across fragmented landscapes and further emphasizes the need to consider the full suite of habitats created in the aftermath of forest fragmentation for a more complete understanding of fragmentation impacts. The results here presented are especially important since the experimental re-isolation of the BDFFP fragments mimics a common situation across the tropics, in which regenerating secondary forests are repeatedly cut well before they reach a late successional stage (Laurance et al. 2007).

The results of chapter 5 show that primary forest specialist bats, which occurred at low abundances in secondary regrowth (Bobrowiec and Gribel 2010) and in forest fragments (Sampaio 2001) ~15 years after the experimental clearing, have also benefited from the increased permeability of the matrix associated with the maturation of the secondary forest in the matrix during the last 15 years. This recovery, matching patterns found for several other taxa, including understory birds and dung beetles (Quintero and Roslin 2005; Stouffer et al. 2011) seems to be dictated by the interaction between species' spatial requirements and their tolerance towards matrix habitats. Following the initial fragment isolation, bird species that persisted in the BDFFP fragments were generally less mobile (Van Houtan et al. 2007) and many of the groups less impacted by the experimental forest clearance, e.g. ants and frogs (Tocher et al. 1997, Vasconcelos and Bruna 2012), have limited spatial needs. In bats, lower fragmentation susceptibility by species with small area requirements was also observed at land-bridge islands in Panama (Meyer and Kalko 2008) and prior to the development of secondary forests in the matrix of the BDFFP bat species with smaller area requirements may have also been the least affected by habitat disruption. With the increase in matrix permeability due to the substitution of cattle pastures by regrowth forests, species capable of crossing or exploiting the matrix seemed to have become further advantaged and currently, mobility in combination with small

body size and phytophagous diet are the best correlates of bat species vulnerability at the BDFFP (Farneda et al. 2015).

The available evidence suggests that the interaction between bats and the landscapes they occupy is bidirectional and that, although bat abundance and occupancy are affected by local habitat structure and landscape composition and configuration, bats also contribute to the spatiotemporal heterogeneity of the landscapes they inhabit. The way bats contribute to landscape "management" still deserves further research attention, but taking the BDFFP as an illustrative example, the interaction between bats and the modified landscapes can be conceptualized in the following way:

i) Initial forest clearing and associated forest fragmentation and deterioration erodes bat assemblages and reduces the occupancy of primary forest specialist bats. This selective filtering leads bat assemblages in forest remnants to be characterized mostly by species with small area requirements, low body mass and a phytophagous diet (Sampaio et al. 2003; Bobrowiec and Gibrel 2010).

ii) Extant populations of frugivorous bats, many of which are specialized in dispersing pioneer tree species (e.g. *Sturnira lilium* and *Carollia perspicillata*), aid initiating and sustaining the successional pathway leading to secondary forest succession (Wieland et al. 2011).

iii) The maturation of secondary forest reduces the degree of contrast between matrix habitats and forest remnants, buffering the impacts of fragmentation and allowing the recolonization of fragments and matrix habitats by primary forest specialists. Many of these primary forest specialists are gleaning animalivorous bats, which by feeding on herbivorous arthropods reduce herbivory levels in regenerating secondary forests, further enhancing secondary forest succession (Fig 1; Chapter 5).

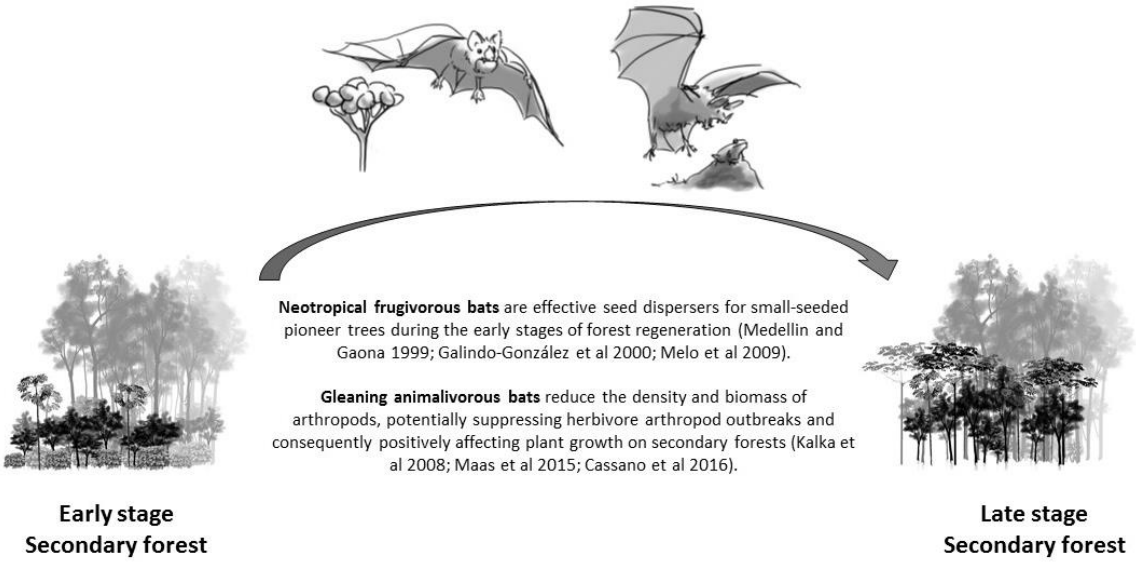

Figure 1 – Contribution of frugivorous and gleaning animalivorous bats to secondary forest maturation. Frugivores actively disperse seeds, helping to initiate and sustain secondary forest succession and gleaning animalivorous bats are likely to support secondary vegetation growth through the predation on herbivorous arthropods.

Conservation implications

In fragmented landscapes, the management of the matrix can aggravate or lessen the impacts of forest loss and forest disturbance. In extremely modified landscapes, the reduced amount of remnant vegetation somewhat limits further forest loss, not only since most of it has already been lost but also because remaining vegetation is often legally protected (Bradshaw 2012; Driscoll et al. 2013). Under this scenario, matrix management, and in particular the management of regenerating (secondary) forest will majorly dictate the future of biodiversity in human-modified landscapes (Melo et al. 2013), including that remaining in fragments of natural vegetation.

The results of this thesis support the view that larger fragments and older secondary forest support assemblages that are more species-rich and more similar to those in non-disturbed habitats. Additionally, we provide evidence that secondary forest regeneration can alleviate fragmentation impacts and that forest specialist species benefit from secondary forest maturation. Therefore, conservation strategies in Neotropical disturbed landscapes should, in addition to ensuring the preservation of large areas of primary forest, promote the regeneration of secondary forest areas. This regeneration of secondary forest areas can take place though a multitude of approaches that form an intervention gradient ranging from spontaneous natural regeneration (passive restoration) to more expensive and labour-demanding tree planting (active restoration) (Holl and Aide 2011). Natural regeneration, the process by which species able to colonize a given area are allowed to initiate forest restauration and create successional trajectories, is a viable, although often overlooked, land-use option that has the potential to restore large areas at low costs (Chazdon and Uriarte 2016). Yet, forest regeneration is a slow process and therefore policies that ensure long-term management of naturally regenerated areas are necessary. A positive example of such policies is given by the Brazilian state of Pará, where secondary vegetation can only be cleared if below 10 m^2/ha of basal area for municipalities with a primary forest cover > 50% or if below 5 m^2/ha for municipalities with a primary forest cover of < 50% (Vieira et al 2014).

Our results further suggest that the retention of large (> 10 ha) fragments can aid in the regeneration and ecological recovery of anthropogenically disturbed forest habitats. As previously mentioned, frugivorous bats, through their role as effective seed dispersers, especially of pioneer plant species (Medellin and Gaona 1999; Galindo-González et al. 2000; de la Peña-Domene et al. 2014) and insectivorous bats, through their role in the reduction of herbivory levels via the control of arthropod populations, can help initiate

and enhance the successional processes and by doing so augment the provision of ecosystem services and improve habitat quality and connectivity in degraded tropical forests. In deforested landscapes, forest fragments guide the movements of frugivorous and insectivorous bats, thus affecting the spatial patterns of seed dispersion and insect suppression. Bats should therefore be considered in the management and restoration of transformed and fragmented landscapes. As Neotropical frugivorous bats use olfaction to detect mature fruits, essential oils from ripe chiropterochorous fruits have been suggested as a possible way to attract bats to degraded areas and therefore increase seed rain (Bianconi et al 2010). Also, as roost shortage may limit frugivorous bat numbers and, by association, the seed-dispersal ecosystem services they provide, the provision of artificial bat roosts has been suggested as one possible way to catalyse bat-assisted forest regeneration (Kelm et al 2008). Yet, recent evidence from Costa Rica indicates that artificial roost provision was unable to accelerate forest regeneration in abandoned pastures and therefore more studies on the efficiency of this method are needed (Reid et al 2013).

This thesis also supports that Neotropical bats can be used as indicators of forest disturbance. Bats, and in particular phyllostomids, are abundant, diverse, and relatively easy to survey, thus fulfilling many of the requirements for indicator taxa (Medellin et al. 2000; Meyer et al. 2016). Here, we show that high species richness, low levels of dominance and high abundance of gleaning animalivorous species are indicative of high habitat quality (vegetation structure and composition more similar to primary forest) whereas assemblages with opposing characteristics (low species richness, high levels of dominance and low abundance of gleaning animalivorous bats) indicate vegetation characteristics associated with disturbed forests.

Study limitations and future research

This study has helped understanding some of the effects of tropical forest fragmentation on the spatiotemporal dynamics of Neotropical bat assemblages. Yet, many topical questions remain to be explored and some can be better clarified by addressing some of the limitations of this study.

A key question to address when investigating the importance of the matrix and forest fragments to tropical bat assemblages in fragmented landscapes is the extent to which the resources inside and outside forest remnants influence fragment occupancy. It is already known that matrix resources can boost the abundance levels of certain species. For instance, abundant fruit availability of *Vismia* and *Cecropia* in the BDFFP secondary forest matrix can augment the abundance of *C. perspicillata* and *R. pumilio*, however, for most species, information about the availability of food or roosting resources in matrix habitats is not available. Take *Trachops cirrhosus* for example, a common carnivorous bat in Amazonian bat assemblages. Although the species is known to prey on anurans at the BDFFP (Rocha et al. 2012; Rocha et al. 2016), to what extent does the abundance of prey in modified habitats influence the species' distribution and abundance levels? Or alternatively, to what extent does roost availability affect the same attributes? This information is lacking even for the most common species and for some of the most intensively studied areas such as the BDFFP.

We focused on assemblage-, ensemble- and species-level responses to habitat modification and showed that for some species abundance responses are sex-specific. However, it would be interesting to investigate species behavioural responses to habitat disturbance, which may represent more sensitive indicators of species' responses to habitat conversion. Bat activity patterns for instance are affected by habitat structure, with

responses being more pronounced in habitats with high structural contrast with primary forest such as open agricultural areas (Presley et al. 2009a) and urban areas (Montaño-Centellas et al. 2015) than in habitats with more similar vegetation structure such as secondary regrowth (Presley et al. 2009a) and reduced-impact logging areas (Castro-Arellano et al. 2009; Presley et al. 2009b). Therefore, the periodical re-isolation of experimental fragments at the BDFFP could be used as a before-after-control-impact experiment to evaluate the effects of secondary forest and small man-made forest clearings on the activity patterns of Neotropical bats.

Equally interesting would be to investigate the levels of genetic connectivity between bat populations inhabiting the BDFFP fragments. Some studies have already analysed how forest disruption affects the genetic diversity of tropical bats. Meyer et al. (2009) for instance, investigated how species with different mobility were affected by fragmentation in a Panamanian land-bridge island system with high fragment-matrix contrast. This study has found that whereas the canopy frugivore *Uroderma bilobatum* did not display lower genetic diversity on islands compared to mainland sites, the less mobile understory frugivore *C. perspicillata* showed reduced genetic diversity on islands, relative to continuous forest. More recently, Ripperger et al. (2014) investigated genetic differentiation in another small frugivore, *Dermanura watsoni*, in fragments surrounded by an agricultural matrix in Costa Rica and McCulloch et al. (2013) addressed the same question focussing on *Artibeus lituratus*, a large, abundant and highly mobile frugivore, in the Atlantic forest. These studies, conducted in systems of relatively low matrix contrast, revealed more modest levels of genetic differentiation than found by Meyer et al. (2009). However, despite indication that fragmentation leads to genetic erosion regardless of fragment-contrast, further studies are needed to assess how matrix

permeability interacts with species' life-history traits in the maintenance of gene flow amongst bat populations in contemporary fragmented landscapes.

Vertical stratification is one of the most important features structuring bat assemblages, allowing for the coexistence of a large number of species in the same geographical area (Bernard et al. 2001; Kalko and Handley 2001; Ramos Pereira et al. 2010; Marques et al. 2015). Yet, although both richness and abundance differ among strata in both continuous forest and forest fragments (Silva 2012), no study has yet offered a comprehensive picture of the effects of forest fragmentation on the vertical stratification of bat assemblages.

Two major study limitations somewhat limit the span of the analysis here presented, namely: i) species inventory completeness and ii) imperfect species detectability.

The sole reliance on mist-netting data for the analyses undertaken for this thesis precludes a complete overview of the impacts of forest fragmentation on the BDFFP chiropteran fauna as a whole since, with the exception of *P. parnellii*, aerial insectivorous bats are not effectively sampled with mist-nets (Kalko 2008). In the Amazon, aerial insectivorous bats are represented by the families Thyropteridae, Furipteridae, Mormoopidae, Emballonuridae, Vespertilionidae, Molosidae and Natalidae (López-Baucells et al. 2016). Ultra-sound sampling was conducted in parallel to the mist-netting whose data was used for this thesis. These data are currently being analysed and form part of an ongoing PhD thesis. Preliminary results have provided the first echolocation description and range expansion of numerous species (e.g. López-Baucells et al. 2014).

The investigation of spatial and temporal trends in species richness or the effects of environmental factors on local species occurrence might be hampered by imperfect and variable species detection (Meyer et al. 2011). Detectability may differ among sample locations, through time, or due to species-specific factors. The failure to formally account

for imperfect detectability potentially leads to the classification of occupied sites as unoccupied (false absences), to the underestimation of abundance or to incorrect inferences about habitat relations or temporal trends (Kéry et al. 2009). Despite possible bias introduced by not accounting for differential species detectability, the vast majority of studies regarding spatial and temporal variation in abundance or occurrence almost never account for it (Royle et al. 2007) and to date, no study addressing the impacts of fragmentation on bat assemblages has taken this important issue into consideration. The analyses here presented could be further expanded by the use of a hierarchical modelling framework for trend estimation in open populations in the presence of imperfect detection (Kéry et al. 2009) or by the expansion of the joint species distribution models used in the chapters 4 and 5 to accommodate detection probability (Beissinger et al. 2016). These models are applicable when counts are available from multiple sites and multiple seasons and there is replication within seasons, being therefore compatible with our sampling protocol.

Concluding remarks

Overall, the results of this thesis, supported by findings in other humanized landscapes (e.g. Meyer and Kalko 2008; Avila-Cabadilla et al. 2012; Cisneros et al. 2015; Chambers et al. 2016; Arroyo-Rodríguez et al. 2016), indicate that the spatiotemporal dynamics of tropical bats in fragmented forests is greatly influenced by the complexity of the vegetation structure at the local-scale and by the amount and configuration of forest cover at the landscape-scale. Spatial and temporal heterogeneity affect the diversity and abundance of food and roost resources, and, through complex, often synergistic pathways,

affect species interactions, behaviour, fitness and ultimately species occurrence and abundance.

At the landscape level, although the results of this thesis highlight the importance of large (> 10 ha) primary forest patches and advanced secondary forest habitats in the conservation of bat diversity, they also stress the irreplaceable conservation value of continuous blocks of old-growth forest. The results here presented therefore add to an increasing body of evidence showing that tropical biodiversity is overwhelmingly dependent on the maintenance of large expanses of primary habitat (Barlow et al. 2007; Gibson et al. 2011). Yet, they also highlight the potential of advanced-stage (> 20-year old) secondary forests to regenerate degraded and fragmented landscapes and therefore protection of advanced-stage second-growth should also be incentivized as it brings considerable benefits to global tropical conservation efforts.

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